SYSTEMATICS AND EVOLUTION OF *CARMICHAELIA*, *CHORDOSPARTIUM*, *CORALLOSPARTIUM*, AND *NOTOSPARTIUM* (FABACEAE) FROM NEW ZEALAND

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Heenan, P.B. 1998: An emended circumscription of *Carmichaelia*, with new combinations, a key, and notes on hybrids. *New Zealand Journal of Botany 36*: 53-63.

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ABSTRACT

All names in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* were typified, with many names requiring the selection of a lectotype. A taxonomic revision was undertaken of *Carmichaelia*, with seventeen species accepted as indigenous to New Zealand. A major taxonomic problem in *Notospartium* was resolved using morphological and habitat data. Two species of *Notospartium* are indigenous to Marlborough, these being separated by fault lines and each is associated with different parent materials.

Wood anatomy of most species of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* was described to provide phylogenetically informative characters. The wood is characterised by vessels with helical thickenings and simple perforations; vessels, axial parenchyma, and short rays arranged in storied structure; predominantly fusiform parenchyma; and rays up to 20 cells wide. Developmental studies showed that *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* exhibit habit- and leaf-heteroblastic development.

A phylogenetic analysis using 47 mainly anatomical and morphological characters was undertaken using parsimony analysis. This analysis provided evidence that *Carmichaelia* is paraphyletic if *Chordospartium*, *Corallospartium*, and *Notospartium* are excluded, but monophyletic if these taxa are included in *Carmichaelia*. It is recommended that *Carmichaelia* be recircumscribed to include *Chordospartium*, *Corallospartium*, and *Notospartium*. Among the outgroup species *Swainsona novae-zelandiae* is shown to differ from Australian *Swainsona* by significant anatomical characters. To more accurately reflect its evolutionary history it is recommended that it be placed in a new and monotypic New Zealand genus.

CHAPTER ONE

GENERAL INTRODUCTION

1.1 INTRODUCTION

This thesis is primarily concerned with the systematics and evolution of the legume genera *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* (the *Carmichaelia* complex). This chapter serves as an introduction to the thesis. It provides an overview of the genera in the study and their taxonomic history and problems, it outlines the discipline of systematics, and presents the objectives of this study.

The thesis is divided into two parts. Part I includes the typification of all names in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* (Chapter 2), followed by a taxonomic revision of *Carmichaelia* and the clarification of a taxonomic problem in *Notospartium* (Chapter 3).

Part II of the thesis is on the phylogeny of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. This part includes the description of the wood anatomy of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*, an assessment of the evolutionary patterns in wood characters, and discussion on evolutionary ecology that emphasises the relationship between wood anatomy and ecology (Chapter 4). The description of heteroblasty provides data for inclusion in the phylogenetic analysis, and also includes further discussion on evolutionary ecology (Chapter 5). In the discussion for wood anatomy and heteroblasty emphasis is given to aspects of their evolutionary ecology because, in developing an evolutionary classification (Chapter 6), it is necessary to understand pragmatic and functional aspects of adaptive radiation and character divergence.

Data from wood anatomy and heteroblasty are included with other anatomical and morphological characters in a phylogenetic analysis of the *Carmichaelia* complex (Chapter 6). This phylogenetic analysis allows for an assessment of species relationships, a critical appraisal of the circumscription of the four genera, and for an indication of the group's closest relatives.

Chapter 7 summarises the conclusions and results and indicates possible avenues

for further research.

The *Carmichaelia* complex belongs to the Fabaceae subfam. Faboideae tribe Carmichaelieae (Hutchinson 1964; Polhill 1981a). The Faboideae includes some 440 genera and 12,000 species. The tribe Carmichaelieae, in addition to the four genera in this study, also includes *Streblorrhiza speciosa*, a monotypic but extinct genus from Phillip Island in the Tasman Sea. The tribe Carmichaelieae and the tribe Galegeae, which includes the Australian and New Zealand *Swainsona* and *Clianthus*, have been considered to be related to the tropical Tephroseae (Polhill 1981a). Recent molecular studies have also indicated that the tribes Carmichaelieae and Galegeae are very closely related (Liston & Wheeler 1994; Sanderson & Liston 1995).

The phylogenetic part of the study includes a number of other genera from the subfamily Faboideae tribe Galegeae (Polhill 1981b) as outgroup taxa. The following list summarises those genera that are included in the different parts of this thesis:

Carmichaelia, as the taxonomy stands prior to this thesis, is represented in New Zealand by 38 species and 8 varieties (Allan 1961), and 1 other species occurs on Lord Howe Island (Green 1994).

Chordospartium includes two species, both of which are endemic to Marlborough (Purdie 1985).

Corallospartium is a monotypic genus from the South Island, although slender plants from Otago have been formally named as a variety (Allan 1961).

Notospartium is also endemic to the South Island and includes two species from Marlborough and one from Canterbury.

Astragalus bisulcatus occurs in North America and is a representative of a large genus of between 2000 (Polhill 1981b) and 2500 species (Sanderson & Wojciechowski 1996). *Astragalus* is placed in tribe Galegeae subtribe Astragalinae (Polhill 1981b).

Clianthus puniceus is endemic to the North Island of New Zealand. It is placed in tribe Galegeae subtribe Coluteinae (Polhill 1981b).

Biserrula pelecinus occurs in the Mediterranean and North Africa and is placed in tribe Galegeae subtribe Astragalinae (Polhill 1981b).

Lessertia perennans and *Sutherlandia frutescens* occur in South Africa. *Lessertia* is a genus with about 50 species and *Sutherlandia* has about 6 species (Polhill 1981). Both genera are placed in tribe Galegeae subtribe Coluteinae (Polhill 1981b).

Swainsona includes 84 species in Australia and a single species, *S. novae-*

zelandiae, in New Zealand (Thompson 1993). It belongs to tribe Galegeae subtribe Coluteinae (Polhill 1981b). Thirteen species of *Swainsona* are included in the study and these are representative of several informal groups recognised by Thompson (1993). The species are *S. cyclocarpa*, *S. decurrens*, *S. formosa*, *S. galegifolia*, *S. kingii*, *S. lessertiifolia*, *S. microphylla*, *S. novae-zelandiae*, *S. oligophylla*, *S. oroboides*, *S. recta*, *S. stipularis*, and *S. swainsonioides*.

1.2 TAXONOMIC HISTORY AND PROBLEMS

The first New Zealand brooms were collected by Joseph Banks and Daniel Solander from Mercury Bay, Tokomaru Bay, Tolaga Bay, and Poverty Bay on the East Coast of the North Island, on Captain Cook's first voyage in 1769-70. Solander, in his unpublished manuscript, *Primitiae Florae Novae Zelandiae*, referred to these specimens as "*Genista compressa*". In 1773 J. G. A. Forster, naturalist on Cook's second voyage, collected specimens at Dusky Sound, and later described and named them as *Lotus*? *arboreus* (Forster 1786). The genus *Carmichaelia* was erected in 1825 by Robert Brown, when he described *C. australis* (Brown 1825).

Between 1825 and 1899 species or varietal names in *Carmichaelia* were published by a variety of authors both resident in and outside of New Zealand. Many of these new taxa were only known from few collections, often from a single locality, and the range of variation within and between species and populations was poorly understood. Kirk (1899) provided the first comprehensive treatment when he described 11 new species or varieties, and he presented a key to 19 species in total.

Simpson (1945) completed a major revision of *Carmichaelia* and he described 14 new species and 5 new varieties, which brought the total number of species to 40 and varieties to 11. Unfortunately, Simpson (1945) failed to typify many names, often did not indicate the correct authorities, and left several complex groups poorly resolved (Zotov 1946). Allan (1961) based his *Flora of New Zealand* treatment of *Carmichaelia* on the revision of Simpson (1945).

The identification of species of *Carmichaelia* is often difficult (Hooker 1864; Kirk 1899; Cheeseman 1906), and the taxonomic status of some species accepted by Simpson (1945) and Allan (1961) is often disputed (Eagle 1982; Druce 1992; Wilson & Galloway 1993). Purdie (1984) suggested that the taxonomy of several closely related

species could be simplified by use of characters from their flavonoid chemistry, and that species boundaries were often related to geographic location, such as the botanical districts of Cockayne (1928), as much as to taxonomic characters.

In *Notospartium* there has been some uncertainty and confusion about the taxonomic status of the two Marlborough endemics, *N. carmichaeliae* and *N. glabrescens*. For example, Eagle (1982: 276) and Wardle (1991: 656) indicated uncertainty about the relationship between these species, Smith-Dodsworth (1991) accepted only one species in Marlborough which he did not name, and Druce (1992) and Wilson & Galloway (1993) treat *N. glabrescens* as a synonym of *N. carmichaeliae*. Furthermore, some authors have accepted two species occurring in Marlborough but have confused them or have misapplied their names. For example, Cheeseman (1914) illustrated *N. carmichaeliae* but the pod figured belongs to *N. glabrescens*, and Salmon (1980, fig. 1, 2, and 9) illustrated under the name *N. glabrescens* a plant, flowers, and bark of *N. carmichaeliae*.

It is apparent from the published literature and personal communications with field botanists that the currently accepted treatments of *Carmichaelia* and *Notospartium* have limitations in terms of their application and practicality. A species level revision of these genera is clearly needed.

The recognition of the segregate genera *Notospartium* (Hooker 1857), *Corallospartium* (Armstrong 1881), and *Chordospartium* (Cheeseman 1911), and their relationship to *Carmichaelia* has also been contentious. These segregate genera have generally been recognised on the basis of a few unique characters and their overall different appearance, without a thorough study of a large number of characters across all species in each genus. There has been some criticism of the validity of recognising four genera (Slade 1952), but an alternative classification has not been formally proposed.

The first to note the similarity of *Carmichaelia* to the segregate genera was Hooker (1857) who, when describing *Notospartium carmichaeliae*, observed that:

> "Its resemblance to *Carmichaelia* is most striking in many respects, and before receiving the fruit from Mr. Waites, I had regarded it as an undetermined species of that genus. Like it, the old plants are leafless, the branchlets slender, grooved, twiggy, compressed, covered with green bark, bearing here and there small tooth-like projections, which are undeveloped bracts, and from some of these small pendulous racemes of flowers, of the aspect and form of *Carmichaelia*, but larger,

> are put forth; it further agrees with that genus in the general character of the calyx, petals, and stamens, but in fruit it widely differs ... Mr. Bentham, who has kindly examined this plant, informs me that it is nearly allied both to *Sesbania* and *Carmichaelia*, and is very important as showing the affinities of the latter genus".

It is significant that Hooker (1857) named the new *Notospartium* as *N. carmichaeliae* because of its resemblance to species of *Carmichaelia*. Hooker (1864) also described *Carmichaelia crassicaule* prior to it being transferred to the new genus *Corallospartium* by Armstrong (1881) on the basis of the "compressed one-seeded pod ... and the fascicled woolly flowers" being different from species of *Carmichaelia*.

When Cheeseman (1911) described *Chordospartium* he made several observations on its close relationship with *Corallospartium* and *Carmichaelia*. Cheeseman wrote:

> "Although I consider that the characters of *Chordospartium* fully justify its erection into a separate genus, it must be confessed that the differences between it and *Corallospartium* are not of a very pronounced type. If however, differences in habit, inflorescence, &c., are not considered sufficient to separate *Corallospartium* and *Chordospartium*, then, by parity of reasoning, similar characters of no greater importance cannot be used to distinguish both of these groups from the section *Huttonella* of *Carmichaelia*, and the three genera must merge into one. Some botanists may prefer this course, for it is very much a matter of taste and personal idiosyncrasy whichever view is adopted."

It is clear from the above quote that Cheeseman felt a certain amount of unease in recognising the new and monotypic *Chordospartium*. While Cheeseman defended the erection of *Chordospartium* as "a matter of taste and personal idiosyncrasy" it is very much an authoritarian approach to taxonomy, and lacks the rigour and logic that would result from a detailed and careful study of all taxa in the group. This can be paraphrased an alternative way: believe what I say and do because my name is Thomas Cheeseman!

Later, Cheeseman (1925) again emphasised the close relationship of the genera by noting that *Chordospartium* is "A very remarkable plant, in some respects connecting the genera *Corallospartium*, *Carmichaelia*, and *Notospartium*."

The above quotes indicate that the characters emphasised by Hooker (1857, 1864), Armstrong (1881), and Cheeseman (1911, 1925) as being of generic importance are mainly those associated with growth habit and, in particular, the shape of the pod. The

special emphasis given to pod shape as a generic character is further highlighted by Kirk's (1899) genus *Huttonella*: "General characters of *Carmichaelia*, but pods indehiscent, very small, turgid or almost inflated, the breadth exceeding the depth; beak short, turned upwards." Cheeseman (1925) reduced *Huttonella* to a section of *Carmichaelia*. In a general discussion on the taxonomic relationships among the New Zealand broom genera Polhill (1981) pointed out "that fruit features are relatively labile in the family and should not be weighted unduly." It is clear that differences in gross pod morphology have been over-emphasised in the generic concepts of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*, and that other floral and vegetative characters should be considered in elucidating relationships at genus level.

Laing & Blackwell (1940) broadened the debate on the relationships of the four broom genera by making the novel suggestion that hybridisation may be involved in the group and, in particular, that *Chordospartium* could be a hybrid between *Notospartium* and *Carmichaelia*. It has also been suggested that *Chordospartium* could be a hybrid between *Notospartium* and *Corallospartium* (Slade 1952). After investigating the cladode anatomy and leaf trace systems of the *Carmichaelia* complex, Slade (1952) concluded that *Chordospartium* and *Corallospartium* shared a close relationship, but contradicting this were the inflorescence, habit, and slender stems of *Chordospartium* which were similar to *Notospartium*. In an assessment of relationships among the broom genera Slade (1953) recommended placing *Chordospartium* and *Corallospartium* as subgenera of *Carmichaelia*, a similar observation to that of Cheeseman (1911), while retaining *Notospartium* as a distinct genus.

It is apparent that as new characters were being discovered that serious doubts were beginning to be cast on the validity of recognising *Chordospartium*, *Corallospartium*, and *Notospartium* as segregate genera of *Carmichaelia*. The discovery of unilocular anthers in *Carmichaelia*, and bilocular anthers in *Chordospartium*, *Corallospartium*, and *Notospartium* provided support for two distinct lineages in the group (Godley 1980). The most recent observation on the relationships of the genera was by Purdie (1985) who, when describing *Chordospartium muritai* as a new species, echoed many of the observations made by earlier authors: *Ch. muritai* "appears to combine the characteristics of the other broom genera, i.e., habit of *Notospartium*, flower colour and size of *Carmichaelia*, and, in common with *C. stevensonii*, abbreviated pods and grooved branches of *Corallospartium*."

Several infrageneric classifications have also been proposed for *Carmichaelia*. The first was by Kirk (1899) who divided *Carmichaelia* into two sections: *Nana* for the dwarf species and *Eucarmichaelia* for the erect or spreading species. Apart from growth habit there are no other characters that support section *Nana*, and the monophylly of the group should be questioned. Kirk's (1899) genus *Huttonella*, erected for several species of *Carmichaelia* with dorsiventrally compressed pods, was reduced by Cheeseman (1906) to a section of *Carmichaelia*, and was treated by Simpson (1945) as a subgenus of *Carmichaelia*. Simpson (1945) erected an elaborate infrageneric classification for *Carmichaelia* when he recognised 8 subgenera on the basis of mainly growth habit, pod, and seed characters.

The placement and affiliations of the woody and shrubby *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* in the tribe Carmichaelieae is also of significant interest. The tribe Carmichaelieae belongs with several other tribes in what has been referred to as the "temperate herbaceous clade" (Lavin et al. 1990) or the "Astragalean Clade" (Sanderson & Wojciechowski 1996), both clades that are dominated by herbaceous species. Therefore, the occurrence of woodiness in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*, when compared to their herbaceous relatives, could enable the development of a hypothesis for the evolution of woodiness in the New Zealand environment. This will be examined in the context of the wood anatomical and phylogenetic studies.

The above discussion serves to emphasise taxonomic difficulties among species of *Carmichaelia* and *Notospartium*, and it also raises many questions about the relationship of *Carmichaelia* to the segregate genera *Chordospartium*, *Corallospartium*, and *Notospartium*. The *Carmichaelia* complex is clearly in need of a taxonomic revision at species and generic level. In particular, detailed attention should be given to characters other than the fruit, and at both genus and species level a more thorough examination should be made of vegetative, floral, and anatomical characters. It is the purpose of this thesis to document and describe new characters and to reevaluate previously described characters in the context of the species level revision of *Carmichaelia* and *Notospartium* and the generic revision of the *Carmichaelia* complex.

1.3 THE AIMS OF THIS THESIS

The discussion in Chapter 1.2 indicates that *Carmichaelia* and *Notospartium* have taxonomic problems at species level, and that the generic concepts and relationships of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* need to be reassessed.

This thesis has two main objectives:

1. To provide a stable and reliable species level classification for the genera *Carmichaelia* and *Notospartium.*

2. To develop a phylogenetic hypothesis for *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium.* This hypothesis will enable the relationships of the four genera to be assessed, and the elucidation of their closest relative. An important, although secondary part of this objective, is an understanding of the evolutionary ecology of the *Carmichaelia* complex using wood anatomical data and heteroblastism characters.

To achieve objective 1, *Carmichaelia* is revised in a traditional taxonomic study, and for *Notospartium* the relationships between morphological variation, distribution, geology, and habitats of the two Marlborough species is examined.

To achieve objective 2 new information from wood anatomy and developmental studies is presented and discussed from the viewpoint of evolutionary ecology. These data are also analysed along with other morphological, cytological, and anatomical characters in a phylogenetic analysis.

1.4 THE PRINCIPLES OF SYSTEMATICS

To undertake a systematic revision it is necessary to understand the different conceptual and procedural aspects of the discipline systematics, and in particular to understand the differences between classification, nomenclature, taxonomy, evolution, and phylogeny. A concise summary of the relationships of the different areas of

systematics has been provided by Stuessy (1979, 1990), a view that is in agreement with other definitions (e.g., Davis & Heywood 1963; Mayr 1969; Darlington 1971).

According to Stuessy the discipline of systematics includes three main areas, the process of evolution, phylogeny, and the taxonomy of the group. Taxonomy includes the process and activities of classification, which is when individuals are grouped into a taxon (e.g., species) and then the taxa are ranked into categories (e.g., genera). Activities associated with classification include the referral of individuals to a particular taxon using characters (identification), and the labelling of a particular taxon with a name (nomenclature). Study of the processes of evolution includes sources of variability, organisation of genetic variability in populations, differentiation of populations, reproductive isolation, and hybridisation. The study of phylogeny involves the divergence and/or development of groups of plants over time, at particular places, and by particular processes.

The purpose of this thesis is to provide a revised species level classification of *Carmichaelia* and to reassess the generic boundaries of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* using phylogenetic methods of analysis. Therefore, it considers two of the three areas of the discipline of systematics, namely species level taxonomy (Part I) and phylogeny (Part II).

In practice, however, the discipline of systematics is not as easily defined or unified as the above summary indicates. After characters have been discovered and described they can be utilised in a number of different ways. For example, characters can be analysed and interpreted in different ways depending on the methods of classification and alternative species concepts adopted. As the different methods of classification and alternative species concepts are particularly relevant to this thesis they are discussed in some detail below. Five main species concepts are currently being used in plant taxonomy, and each of these are discussed and evaluated in Chapter 1.4.2. The discussion that follows is on the different approaches to developing a classification.

There are currently three major approaches to classification: phenetic classification (Sokal & Sneath 1963; Sneath & Sokal 1973), cladistic classification (Hennig 1966; Wiley 1981), and evolutionary classification (Darwin 1859; Simpson 1961; Mayr 1969; Stuessy 1987). Each of the three methods of classification has strengths and weaknesses, and the application of each is usually dependent on the individual preferences and taxonomic philosophy of the researcher.

Phenetics classifies organisms on the basis of their overall similarity, and this is calculated from numerous characters. In order to make the method objective every character is given equal weight, so that no character is more important than any others. A large number of characters are used because if a character is left out this amounts to the weighting of the characters selected. Each character is recorded as a single numerical value for each taxon, and a data matrix formed. The clustering of species and the formation of similarity classes is calculated by algorithms, and the diagram depicting this relationship is called a phenogram. The phenetic distances can be converted directly into a classification.

Cladistics classifies organisms by the recency of common descent using a phylogenetic hypothesis, and membership of a particular taxon is on the basis of shared and derived characters. The classification is based exclusively on the branching pattern of the phylogeny (e.g., Cantino et al. 1997). The cladogram is converted directly into a classification and only monophyletic taxa are accepted. Two principles are applied to the conversion of a cladogram into a classification. All branchings are bifurcations that give rise to two sister groups, and branchings are usually connected with a change in categorical rank.

Evolutionary classifications are based on observed similarities and differences among different taxa, and these are evaluated in the light of their evolutionary history. A phylogenetic hypothesis is central to understanding the evolutionary history of a particular group of plants. The classification system considers all available data pertaining to the taxon, including features such as the amount of divergence, the uniqueness of the individual characters and character combinations, and characters associated with radiation into different adaptive zones. Evolutionary classifications consider the phyletic divergence of all lineages, since the evolutionary history of sister groups can be very different.

The above summaries for each method of classification indicate that there are fundamental differences in the philosophies and practices of the different methods of classification, particularly between the evolutionary and phylogenetic schools of thought. This has been much debated in the recent literature (e.g., Cronquist 1987 v's Donoghue & Cantino 1988; Hedberg 1995, 1996 v's Snow 1996). The evolutionary and phylogenetic taxonomists agree that a phylogeny must precede a classification, but they differ in a number of other areas. For example, what information is considered in the

recognition of groups of taxa and in how the classification is constructed.

One author, Janvier (1984), considered that the evolutionary and cladistic schools of classification differ in five areas which I now summarise and evaluate.

Firstly, the expression of morphological gaps. Evolutionary taxonomists express morphological gaps between taxa, whereas phylogeneticists emphasise shared and derived characters. The morphological gap concept is a key component of evolutionary classification as it implies character divergence within and between lineages. I regard the characters that support the morphological gap as representing shifts in the evolution of a group, and these groups therefore sometimes warrant formal recognition. Phylogenetic taxonomists classify taxonomic characters and their origin, and give considerable emphasis to branching patterns and sister group relationships, paying little attention to gaps between taxa.

Secondly, species diversity. For evolutionary taxonomists a taxon containing a large number of species merits higher rank than a taxon containing only a few species. This concept is rather unusual as it is unrelated to characters, phylogeny, and other biological attributes, which are the key components in determining rank. Furthermore, it does not consider that the taxon that has a few species may have been subjected to extinctions or limited opportunities for adaptive radiation. For phylogenetic taxonomists rank is assigned to groups that have shared and derived characters.

Thirdly, the use of ecology. Evolutionary taxonomists provide information about ecology and the adaptive zones of taxa. They utilise this information as, for example, radiation into a new adaptive zone is often considered to be closely linked to the acquisition of new characters. A phylogenetic analysis can be used to provide a framework for establishing a relationship between ecological attributes and plant characters, and adaptive radiations and evolutionary trends can be explored. Phylogenetic taxonomists do not use ecological data as they claim that such data mask phylogenetic relationships.

Fourthly, the definition of monophyly. For evolutionary taxonomists a monophyletic group does not have to include the ancestor and all of its descendants. They emphasise ancestor-descendent relationships and accept paraphyletic groups. Phylogeneticists accept only an ancestor and all of its descendants. I believe that taxa are descended from within another taxon of equal rank, and therefore I accept paraphyletic taxa. As I accept that biological evolution occurs, it is logical that a new

taxon would evolve from within a component of another taxon. It is clearly illogical to argue that, for example, a genus can only be monophyletic, as each monophyletic taxon has to have an immediate ancestor which must be in a different genus, and which is then paraphyletic. Recent proposals to replace the Linnaean Classification system of hierarchical classification with a phylogenetic system (de Queiroz & Gauthier 1990, 1992, 1994; Cantino et al. 1997) that recognises clades are aimed at avoiding the conflict between paraphyletic and monophyletic groups.

I consider that phylogenetic classifications are very restricted in accepting only monophyletic taxa that are descendants from the most recent common ancestor and which are supported only by synapomorphies. By ignoring character divergence, ancestor-descendent relationships, autapomorph characters, and ecological and biogeographical attributes, the phylogenetic taxonomists are overlooking complete sets of data and basing their classifications only on the branching patterns of their cladograms. Recognising taxa on the basis of the branching pattern alone clearly ignores other biological attributes that should be considered in a classification.

Fifthly, the significance of fossils. Phylogeneticists base their phylogenies on extant taxa, whereas evolutionary taxonomists consider fossils the best means of establishing relationships and reconstructing the history of a group. This is not necessarily true as many evolutionary taxonomists, myself included, support the need for classifications to be based on a phylogenetic analysis using extant taxa as outgroups. A practical limitation of fossils is that many groups are not represented by fossils or if they are the fossils are often incomplete and therefore lacking important plant parts.

1.4.1 Evolutionary classification

In this thesis the analyses of species and generic level relationships in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* are based on the evolutionary systematics school (e.g., Darwin 1859; Simpson 1961; Mayr 1969; Stuessy 1987). In the discussion that follows I examine in more detail the principles and practices of the discipline of evolutionary taxonomy and I defend my preference for this method of classification.

The guiding philosophy for evolutionary classification is given by Darwin (1859: 369), in the often quoted paragraph:

"But I must explain my meaning more fully. I believe that the *arrangement* of the

groups within each class, in due subordination and relation to each other, must be strictly genealogical in order to be natural; but that the amount of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders." In this statement Darwin emphasised that genealogy and the degree of divergence were both important in the formation of a formal classification.

The principles of evolutionary systematics, developed from the framework advocated by Darwin (1859), have been summarised into four main areas by Stevens (1986). Firstly, a classification should reflect both cladistic and patristic elements of evolution, and be made of predictive taxa. Therefore, it is essential for relationships of all the different parts of the study group to be fully understood, with particular emphasis being given to the number and types of characters that support groups.

Secondly, taxa are formed of members that share several correlated characters. Primitive and derived characters are often not distinguished, and some characters are given more importance than others. Although primitive and derived characters are sometimes not distinguished, I believe that many evolutionary taxonomists have realised the value of synapomorphies, in comparison to symplesiomorphies, and probably given these considerable emphasis.

Thirdly, rank is proportional to the magnitude of the differences between taxa, but the larger the taxon the smaller the gap between it and other taxa need be. The assumption here is that the more taxa there are the more likely it is that there are more character state reversals and other changes and, therefore, in larger groups a smaller number of characters assume increased taxonomic importance. Differences between taxa are usually based on a combination of the total number of characters and the taxonomic significance given to the individual character.

Fourthly, higher taxa show ancestor-descendent relationships. The more characters two taxa have in common, the closer their relationship is considered to be, and the less time since divergence. Furthermore, for evolutionary taxonomists emphasis on ancestor-descendent relationships may help explain the origin and transformation of a character and its functional significance.

As indicated by Darwin (1859) and Stevens (1986) it is essential to understand the

genealogy (phylogeny) of the group being studied before an evolutionary classification is formed. A phylogenetic history must precede the construction of a classification since this allows for the identification of natural groups that share characters in common, the assumption being that they are descendent from a common ancestor. The development and application of phylogenetic methods, and in particular the use of complex computer algorithms for the construction of phylogenetic trees (cladograms), has provided evolutionary taxonomists with explicit, robust, and repeatable methods for developing and testing hypotheses of relationships among and within plant groups. The contribution of the phylogenetic methods of data gathering and analysis have clearly been very significant in the recent development of evolutionary classification methods.

Although evolutionary taxonomists use phylogenetic methods to construct and analyse their data there is a subtle but important difference in the selection of characters. Evolutionary taxonomists include autapomorph characters in their analyses whereas phylogenetic taxonomists exclude these characters. Autapomorph characters are included in analyses by evolutionary taxonomists because they are considered to provide important information for a particular taxon.

When the phylogenetic relationships among the different taxa have been established it is then appropriate to develop a classification. Four dimensions to constructing an evolutionary classification have been identified by Stuessy (1987).

The chronistic dimension. This is usually measured in millions of years and can be measured by the fossil record, major geological events, or using a molecular clock. This dimension is often difficult to apply and develop explicit hypotheses for because it does not directly apply to the physical and visible attributes of the plant group. Nevertheless, it can provide significant insights into the origin and timing of newly acquired characters and of evolutionary processes.

The cladistic dimension. This is the branching pattern of the phylogeny, and includes the sequence of branching of evolutionary lines. A phylogeny provides an explicit hypothesis of relationship and the naturalness of taxa. It indicates the degree of relationship graphically, by grouping taxa that are closely related and separating those that are more distantly related.

The patristic dimension. The total amount of evolutionary changes along the branches of a phylogeny. The patristic dimension gives an indication of the degree of evolution within lineages, and whether some lineages have evolved more rapidly than

others. This dimension provides a framework for recognising groups of taxa and character variation within particular lineages.

The phenetic dimension. This is a measure of overall similarity of the taxa, and is used to establish similarity classes for the construction of a classification.

A particularly important aspect of the evolutionary method is that for the formation of groups it also considers other attributes such as shifts into new adaptive zones, the rate and amount of evolutionary change, and geographic and reproductive isolation. The taxon is seen as a complex organism for which every aspect of its biology is considered to be important in its formation and function. All aspects of the taxon are interrelated and connected to some degree, and therefore I consider it important to include as many aspects of its biology in the processes of identifying groups and assigning rank. Basing a classification on as many aspects of an organisms biology as possible can only assist in ensuring a stable, robust, and informative classification is developed.

In the actual construction of a classification system the evolutionary and phenetic schools of thought are alike in that they accept taxa which are divergent, have undergone anagenesis, or are paraphyletic. However, the phenetic approach, in which groups are formed by the overall similarity of the taxa, is severely limited in that groups may not be defined by synapomorphies. In evolutionary classifications unique characters (autapomorphies and synapomophies) that support a particular taxon are considered important, even if a taxon shares some characters (symplesiomorphies) with other taxa.

Unfortunately, evolutionary taxonomists do not have a standard, repeatable, and testable method to develop classifications; the development of a classification can be very much at the whims and personal preferences of individual taxonomists as to what biological attributes they emphasise. However, this problem is in part negated by evolutionary taxonomists usually considering data from a number of sources. The advantage of this approach is that when data from several sources are congruent it is more likely that a proposed classification reflects natural relationships. I believe this is a much more robust method of developing a classification than the phylogenetic school which uses character branching patterns and synapomorphies alone.

In summary, I consider that evolutionary taxonomy provides the basis for classifications that reflect branching, divergence, and similarity of taxa in the most

pragmatic way. Evolutionary classifications combine the best components of phylogenetic and phenetic taxonomy. Furthermore, because such classifications consider a wide range of the biological attributes of taxa, they have a much higher information content than those of phenetics and cladistics.

1.4.2 Species concepts

Another major problem in systematics is the grouping of individuals into a taxon, and in particular the differing concepts of what constitutes a species (e.g., Levin 1979; de Queiroz & Donoghue 1988; Luckow 1995; McDade 1995), and also a genus (e.g., Just 1953; Lemen & Freeman 1984). At least five species concepts are in common usage.

The need for several species concepts for plants has arisen because the patterns of variation are so diverse and complex, and there are different evolutionary processes that can lead to the origin of new taxa, that no one concept or definition can suffice. Different origins for taxa and patterns of variation in breeding systems, morphology, genetics, and ecology have resulted in a number of concepts to be proposed for the grouping of individuals into a species. For a particular taxon each concept emphasises different evolutionary processes and biological attributes.

Furthermore, there are significant philosophical issues, particularly on the nature of reality. Organisms are real, but can they be grouped and placed in a species? Are species real? Two main views on this issue have been offered. Firstly, species are not real, but are artificial and arbitrary constructions designed to accommodate the need to group and classify organisms. Secondly, species really do exist, they are not arbitrary, and they can be defined by having a unique origin, a spatio-temporal existence, and internal cohesion. I believe that species are real and that their unique origin, spatial and temporal existence, and internal cohesion is reflected in a unique combination of morphological and genetic attributes.

The species category, whether it is applied to arbitrary or natural groups, is a very important and the most used category for the ranking of taxa. There are five species concepts that are in current usage (e.g., Stuessy 1990), and these are described and assessed below.

Firstly, the morphological species concept recognises species on the basis of morphological characters alone. This concept relies on morphological discontinuities to

reflect the biological limits of isolation, interbreeding within and between populations, and genetic divergence (Stuessy 1972). It is not constrained by needing to understand how morphological discontinuities arise or are maintained — if discontinuities exist they can be used to recognise taxonomic units. It is assumed that morphological relationships reflect genetic and reproductive relationships of a similar degree. This concept can also accommodate natural variation as this is to be an expected and obvious outcome of dealing with populations. In practice, as most revisions lack reproductive data, the morphological species concept relies almost entirely on morphological cohesiveness and distance from other taxa.

The morphological species concept has also been defined as: "species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (Cronquist 1978), and "species may be defined as the easily recognisable kinds of organisms, and in the case of macroscopic plants and animals their recognition should rest on simple gross observation such as any intelligent person can make with the aid only, let us say, of a good hand lens" (Shull 1923: 221). Although the morphological species concept is apparently narrow, of antique quality, and is simple to apply it has served taxonomy well in enabling pragmatic and efficient systems for information retrieval in most flowering plants (Burger 1975). This concept has also been known as the classical phenetic species concept (Sokal 1973) or the Linnean or classical species concept (Burger 1975).

Secondly, the biological species concept (Mayr 1969). In this concept species are recognised as a group of interbreeding populations which are reproductively isolated from other such groups. This concept is difficult to apply as in practice there is usually a lack of data about the reproductive isolation and interbreeding of populations. There is often a disparity between the breeding system, morphology, and ecology. These three biological attributes are not necessarily linked, and morphology and ecology may sometimes be more important than breeding systems. Reproductive isolation is more complicated than the simple inability to cross as there are a significant number of other ecological factors related to reproductive isolation. For example, in species that are able to cross there may be significant differences in pollination vector, phenology, spatial and temporal factors, and the ability of hybrid progeny to compete in the natural environment.

Thirdly, the genetic species concept (cf. Stuessy 1990). Species are recognised by

genetic differences or distance among populations or groups of populations. This concept is difficult to apply as rarely are data available on the real genetic differences between populations. The limiting factor for the application of this concept is the amount of intra- and inter-population data that is needed for the genetic analyses.

Fourthly, the evolutionary species concept (Simpson 1961). Species are recognised as a lineage evolving separately from others and with its own evolutionary role and tendencies (Simpson 1961). This concept avoids the need for data on interbreeding and gene flow, allows for some interspecific hybridisation, and considers a "role" to be equivalent to a niche. A difficulty with this concept is that it is necessary to understand relationships among populations. The relationship of the taxon to its environment is important, but this is often difficult to quantify. For example, species of *Carmichaelia* generally occur on very similar dry, alluvial or rocky habitats, and in low rainfall areas. There will be subtle differences in the habitats of the different species of *Carmichaelia* but these are difficult to quantify.

The relationship between the taxon and its environment has been expanded by van Valen (1976) into the ecological species concept where "a species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range".

Fifthly, the phylogenetic species concept (Wiley 1978; Donoghue 1985; Stuessy 1990). This concept is based on a species being a single lineage of ancestral descendant populations which maintain their identity from other such lineages, and that has its own evolutionary tendencies and historical fate (Wiley 1978). Species are monophyletic and can be recognised by shared and derived characters; species contain all and only the descendants of a common ancestor, and are characterised by synapomorphies and apomorphic changes within single branches of a cladogram. This concept was developed as other species concepts were considered not to be able to confidently yield monophyletic taxa. The difficulty of application for this concept is that a large number of populations would need be sampled and analysed by phylogenetic methods to identify particular lineages.

Among practising taxonomists the morphological species concept is the most often used (Stuessy 1990). In a survey of 104 published monographs only 28 included discussion on species concepts (McDade 1995). Twenty-one authors used

morphological differences to distinguish species, and of these fifteen specified that they adopted the morphological or taxonomic species concept of Du Rietz (1930), Davis & Heywood (1963), Cronquist (1978), or Grant (1981). Several authors indicated that the morphological differences on which they relied were assumed to have a genetic basis or be under selection, and others indicated that species were expected to have a distinctive geographic range and/or habitats and ecological coherence.

The species concept adopted in this thesis for the *Carmichaelia* revision and the treatment of *Notospartium* is termed the *morphological species concept* (sensu Stuessy 1990). Discussion on its application to *Carmichaelia* and *Notospartium* is provided in Chapter 3.4.

PART I: TAXONOMIC REVISION

Part I of the thesis includes the typification of all names that have been published in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* (Chapter 2), and the taxonomic treatment of *Carmichaelia* and *Notospartium* (Chapter 3).

The typification of each name is presented separately from the formal taxonomic revision because of the large number (74) of names that are typified and the space that is often required for explanation and discussion on the selection of the type specimen. If the typification of each name was included with the taxonomic treatment, parts of that treatment would be difficult to follow because of the typification of synonymous names. Furthermore, typification is a specialised procedure within taxonomy that is governed by Articles 7-10 in the International Code of Botanical Nomenclature (Greuter et al. 1994).

CHAPTER TWO

TYPIFICATION

2.1 INTRODUCTION

The correct application of the names of taxa of the rank of family or below is governed by nomenclatural types. It is necessary for each name to have specific type, and this is usually a single specimen or illustration. A type is a constituent element of the taxon to which the name is permanently applied. It is only names and not species that have a specific type, therefore typification is nomenclatural procedure. The procedure for the typification of plant names is an essential precursor to a formal taxonomic revision as each name can have only a single type specimen, and this indicates to what taxon the name should apply. The process of typification is governed by the International Code of Botanical Nomenclature (ICBN), Articles 7-10 (Greuter et al. 1994).

The ICBN recognises six main kinds of types (ICBN Art. 9). A holotype is one specimen or illustration used or designated by the author at the time of publication of a name. A lectotype is a specimen or illustration designated as the type when no holotype was indicated at the time of publication, when the the holotype is found to belong to more than one taxon, or when the holotype is missing. An isotype is a specimen that is a duplicate of the holotype specimen. A syntype is any one of two or more specimens cited at the valid publication of a name (protologue) when no holotype was designated. A paratype is a specimen cited in the protologue that is neither the holotype nor an isotype, nor one of the the syntypes if two or more specimens were simultaneously designated as types. A neotype is a specimen or illustration selected to serve as the type when all of the material on which the name is based is missing.

Other terms not specifically defined in the ICBN are isolectotype and isoneotype, these are the respective duplicates of the chosen lectotype and neotype. A lectoparatype has been defined by Brummitt (1985) as a specimen chosen from among the syntypes to be a paratype after lectotypification.

New names in *Carmichaelia, Chordospartium, Corallospartium,* and *Notospartium* have been published intermittently since 1825. The designation of the

type specimen for these names varies. Many early names do not have a designated type but only syntypes. For other names a holotype was designated but this often comprises plant material collected (a) from different plants; (b) on different days; (c) from different localities. Such a holotype collection contravenes the ICBN where it specifies that the holotype should usually be a single collection (ICBN Art. 8.1, 9.1), that would have been collected from one plant, on one day, and at the one locality. It is necessary for the types of all names published in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* to be checked and where necessary for further typification to be undertaken.

2.2 MATERIALS AND METHODS

Type material of all species and variety names published in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* was obtained from AK, BM, CHR, K, GOET, P, S, and WELT. If a holotype specimen was clearly indicated at the time of publication of a name it was only necessary to confirm congruence between the type specimen, herbarium label annotations, and the protologue. Where lectotypification or neotypification is necessary the appropriate articles (Art. 7-10) of the ICBN (Greuter et al. 1994) are followed.

Different names that are based on the same type specimen are homotypic synonyms and are indicated by ≡. Abbreviations of periodicals follow Lawrence et al. (1968), of books Stafleu & Cowan (1976, 1979, 1983), and of names of authors Brummitt & Powell (1992).

2.3 SIMPSON'S TYPE SPECIMENS

Simpson (1945), who described 14 new species and 8 new varieties of *Carmichaelia*, had a standard procedure for choosing type specimens. It is appropriate to review this procedure as background to the typification of Simpson names that follows.

After collecting or receiving plant material Simpson gave the collection a unique number, and prepared pieces for his herbarium and cuttings for propagation. Simpson regarded the common origin of plant material as being of utmost importance, and so

specimens gathered at a later date from the cultivated plant were given the same collection number as the original wild accession. Simpson's numbering system was based on two sets of numbers: e.g., specimen 224/246 is the type for *Carmichaelia floribunda* G.Simpson - 224 is the generic number for *Carmichaelia* and 246 refers to a particular collection.

When Simpson described a new taxon he was very clear in specifying the collection number of the type specimens; e.g., for *C. astonii*, "Type specimens - No. 103 ex author's herbarium." It was customary for Simpson to have a large suite of type specimens, and a special effort was made to collect fruiting, flowering, and often leafy material. This material could have been collected from wild or cultivated plants, from different localities, and on different dates. He did not designate a particular sheet as the type.

It is possible to distinguish a wild collection from cultivated pieces, as the former are often in rougher and weathered condition and have dead, damaged, or broken stems. The cultivated pieces are usually free from such blemishes, and their internodes and branchlets are often longer as a result of good growing conditions.

The type specimens were sent to the herbarium of the Plant Research Bureau, Wellington (then BD, now CHR). It appears that they were received unmounted, as each suite includes only one label in Simpson's hand, and they are mounted on sheets commonly in use during that period. Typically a flowering, a fruiting, and - when available - a leafy piece were mounted on each sheet. They were given a BD number, Simpson's handwritten label was usually placed on sheet A, and identical duplicate labels were placed on the other sheets, which were numbered B, C, etc. For some taxa duplicate sets of specimens were sent to the Auckland Institute and Museum (AK).

Allan (1961) typified most of Simpson's new taxa by selecting a particular sheet as the type. However, many of the sheets selected by Allan comprise pieces collected on different dates and from different locations. Consequently, further lectotypification is necessary. If at least some pieces are dated this is generally a straightforward procedure.

However, some sheets have no dates, and it is the knowledge of Simpson's preparation procedure for type specimens that allows the lectotype to be selected. For example, Allan (1961) selected CHR 45810A as the type for *C. lacustris*. The date of collection is given as Feb 1939. When the pieces on this sheet and the protologue are considered together it is apparent that at least two collections are represented. The

protologue reads "In the type habitat the branches are short and stiffly erect ... in cultivation they are often longer and procumbent, with only the tips ascending." On the type sheet selected by Allan (1961) (Fig. 2.1) the upper and lower left-hand pieces (A) correspond with the description of plants from the wild, and the other two pieces correspond with cultivated plants. The two cultivated pieces differ in that one is in fruit (B) and the other in flower (C), and these are almost certainly from different collections.

The cultivated pieces of *C. lacustris* can be directly compared with other Simpson types where flowering and fruiting pieces were clearly collected on different dates. For example, a label in Simpson's hand on an isolectotype (CHR 45708A) of *C. angustata* var. *pubescens* has different collection dates for fruiting and flowering pieces (Fig. 2.2).

Simpson (1945) also listed, under the heading "Specimens", herbarium sheets examined as part of his revision. These are considered to be type material (i.e., syntypes or paratypes), but their exact status is not indicated here because of the numerous specimens listed and the abundance of extant lectotype material. Simpson's "specimens" are regarded as being equivalent to "representative specimens" - a phrase used to indicate sheets examined by the author and regarded as being representative of the species (e.g., Garnock-Jones 1993; Molloy 1994).

2.4 TYPIFICATION OF NAMES IN *CARMICHAELIA*

***Carmichaelia* R.Br.**, *Bot. Reg. 11*: *t.* 912 (1825)

TYPE SPECIES: *C. australis* R.Br.

TYPE COLLECTION: See 9 below.

1. ***Carmichaelia acuminata*** Kirk, *Stud. fl. New Zealand*, 114 (1899). TYPE COLLECTION: "North Island: White Rock, East Coast, *T. K.*" LECTOTYPE (chosen here): *T. Kirk*, WELT 26239! ISOLECTOTYPE: WELT 26238!, K (photograph seen). LECTOPARATYPES: AK 4918!, WELT 29660!

≡ *C. flagelliformis* Benth. var. *acuminata* (Kirk) Cheeseman, *Man. New Zealand fl.*, 117 (1906).

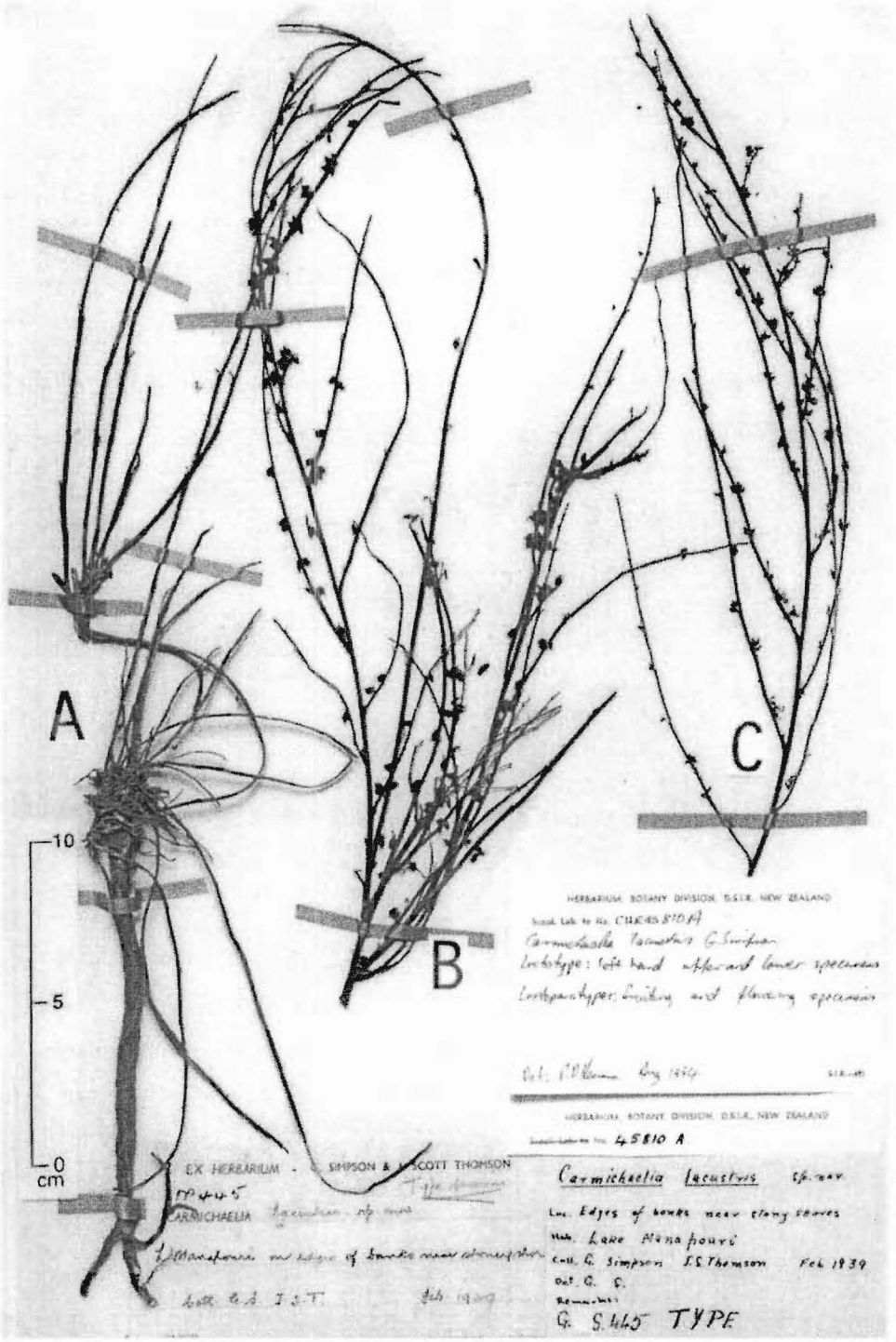
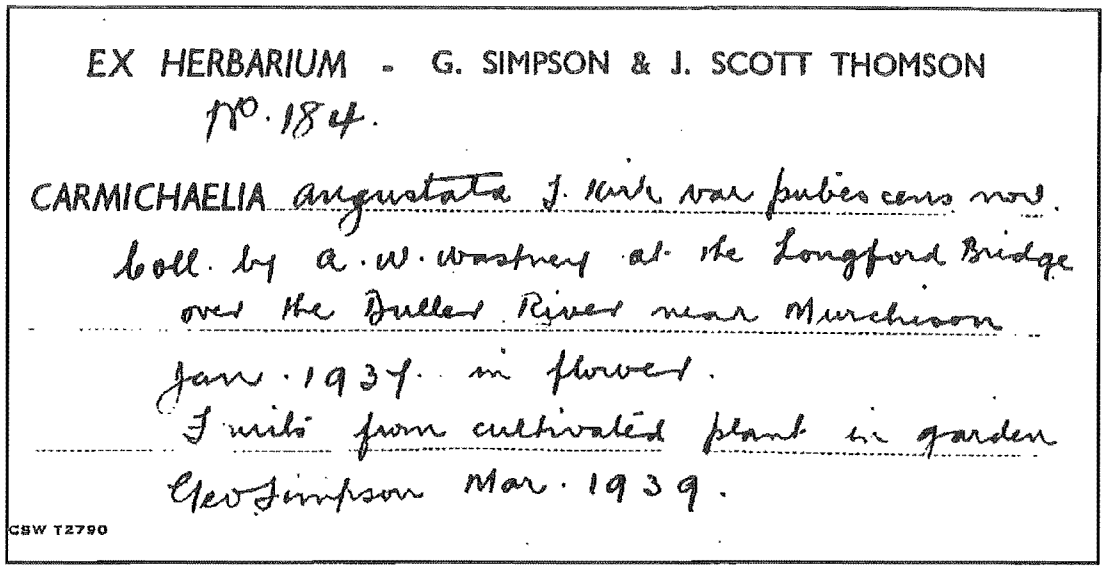


Fig. 2.1 Lectotype sheet for *Carmichaelia lacustris*: **A**, wild-collected pieces; **B**, cultivated fruiting piece; **C**, cultivated flowering piece.


EX HERBARIUM - G. SIMPSON & J. SCOTT THOMSON

No. 184.

CARMICHAELIA angustata J. Kirk var pubescens nov.

coll. by A. W. Anstey at the Longford Bridge over the Buller River near Murchison

Jan. 1937. in flower.

Fruits from cultivated plant in garden

Geo Simpson Mar. 1939.

CSW T2790

Fig. 2.2 A label in G. Simpson's hand indicating different collection dates for pieces of *Carmichaelia angustata* var. *pubescens*: flowering piece collected Jan 1937, and fruiting piece Mar 1939.

Notes: Allan (1961:384) indicated that the type was at WELT, but he did not select one of the three sheets collected by Kirk from White Rock. The lectotype and isolectotypes are similar in having very dark, almost blackened pods, and are certainly from the one collection.

2. ***Carmichaelia aligera*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 250-251 (1945). TYPE COLLECTION: "No. 360 ex the author's herbarium, from a plant in cultivation, collected by Miss L. B. Moore at Anawhata." LECTOTYPE (chosen here): CHR 45532A! fruiting piece, labelled (1). ISOLECTOTYPES: AK 103140!, CHR 45532C-H! LECTOPARATYPES: AK 103140!, CHR 45532A, C-H!, WELT 79546!

Notes: Allan (1961:381) selected CHR 45532A as the type. This sheet comprises one flowering and one fruiting piece, and although the collection dates for these are not given they are almost certainly different. Indirect evidence of this is provided by CHR 211586 and CHR 211588, later collections of *C. aligera* labelled in Simpson's hand

"No. 360 ... (cotype) ... from a plant in cultivation collected by Miss L. B. Moore at Anawhata Fruits March 12 1948" and "Flowers Dec 1947." These pieces are directly comparable to those of the type specimens numbered CHR 45532A and C-H, and provide strong evidence of two different collection dates. Accordingly, I reject Allan's typification, and a second lectotypification is necessary.

3. ***Carmichaelia angustata*** Kirk, *Stud. fl. New Zealand*, 114 (1899). TYPE COLLECTIONS: "South Island: Nelson: valley of the Buller; especially plentiful near the Lyell Junction; *T. K.*" LECTOTYPE (chosen here): valley of the Buller, *T. K.*, WELT 26534! LECTOPARATYPES: AK 4903!, WELT 26528-26532!

Notes: Allan (1961:379) indicated that the type was at WELT, but did not specify a particular sheet. The lectoparatypes were collected from the junction of the Lyell and Buller rivers.

4. ***Carmichaelia angustata*** var. ***pubescens*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 243 (1945). TYPE COLLECTION: "No. 184 ... collected at the Longford Bridge, near Murchison, by Mr. A. W. Wastney." LECTOTYPE (chosen here): *A. W. Wastney*, CHR 45708C! flowering piece. ISOLECTOTYPES: AK 102866!, CHR 45708A, B!, WELT 79545! LECTOPARATYPES: CHR 45708A, B!

Notes: Allan (1961:379) selected CHR 45708A as the type. This sheet comprises fruiting and flowering pieces collected on two different dates (Fig. 2.2). For this reason I reject Allan's typification, and a further lectotypification is necessary.

5. ***Carmichaelia appressa*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 263-264 (1945). TYPE COLLECTION: "Ellesmere Spit, No. 278." LECTOTYPE (*fide* Allan 1961:387): CHR 45580A! ISOLECTOTYPES: AK 70625!, CHR 45580B, E!, WELT 79544!

6. ***Carmichaelia arborea*** (Forst.f.) Druce, *Bot. Soc. Exch. Club Brit. Isles 4 Supplement 1916*, 612 (1917) ≡ *Lotus arboreus* Forst.f., *Fl. ins. austr.*, 52 (1786). TYPE COLLECTION: "Noua Zeelandia." LECTOTYPE (chosen here): 169, 278, Forster, Lotus

arboreus, BM (photograph seen). ISOLECTOTYPES: GOET, K (photographs seen).

Notes: Richard (1832) provided a more detailed location, taken from the "Forster mss": "Crescit in Novae-Zeelandiae loco dicto Dusky Bay. (Forster.)."

7. ***Carmichaelia arenaria*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 252-253 (1945). TYPE COLLECTION: "... on limestone rock at Punakaiki, Westland ... No. 69." LECTOTYPE (chosen here): *G. S., J. S. T., & Dr. McKay*, CHR 45521A! fruiting piece, labelled (1). ISOLECTOTYPES: CHR 45521B-F!, WELT 79543! LECTOPARATYPES: CHR 45521A-F!, WELT 79543!

Notes: Allan (1961:384) selected CHR 45521A as the type. This sheet comprises one flowering, one fruiting, and one leafy piece, and the collection date is given as Feb 1936. These pieces were almost certainly collected on different dates.

Fruiting pieces have been gathered from the type locality by Simpson in Jan 1937 (CHR 18559) and by A. W. Purdie in Feb 1986 (CHR 421331, 432334). In addition, Simpson gathered a flowering piece from his garden in Dec 1946 (CHR 213001). Thus, it is most likely that the fruiting pieces among the type suite were collected during Feb 1936, and the flowering and leafy pieces are different collections, probably from cultivated plants. I therefore reject Allan's (1961) typification, and a further lectotypification is necessary.

8. ***Carmichaelia astonii*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 276-277 (1945). TYPE COLLECTION: "Limestone in the Ure and Inner Clarence Valleys and their tributaries, and at Weld Cone, Marlborough ... No. 103." LECTOTYPE (chosen here): *G. Simpson 103*, CHR 45808A! fruiting pieces, labelled (1) and (2). ISOLECTOTYPES: AK 70629!, CHR 45808B!, WELT 79542! LECTOPARATYPES: AK 209769!, 70629!, CHR 45808A-B!, WELT 79542!

Notes: Simpson (1945) annotated AK 70629 as "co-type." This sheet originally consisted of two collections: flowering pieces from G. Simpson's garden at Dunedin, and fruiting pieces from Isolated Hill, Ure River, Marl., Feb 1937.

Three sheets (CHR 45808A-B, WELT 79542), including the type selected by

Allan (1961), also comprise both flowering and fruiting material. These are almost certainly from two different collections, and as the fruiting pieces on the CHR sheets are very similar to AK 70629 they are presumably from a single wild collection. Consequently, I reject Allan's typification and a further lectotypification is necessary.

9. ***Carmichaelia australis*** R.Br., in J. Lindley, *Bot. Reg. 11*, t. 912 (1825). TYPE COLLECTION: Not stated. LECTOTYPE (chosen here): illustration 912, *Bot. Reg. 11* (1825).

Notes: Lindley (1825) observed that Brown had examined specimens from Colvill's Nursery, Banks & Solander's unpublished "Genista compressa", and Forster's *Lotus arboreus*. As *Lotus arboreus* refers to a different species it is excluded from being a syntype. No specimens of "Genista compressa" at BM and K appear to have been annotated by Brown as *Carmichaelia australis*, so it is most appropriate to select the illustration as lectotype.

10. ***Carmichaelia australis*** var. ***alata*** Kirk, *Stud. fl. New Zealand*, 110 (1899). TYPE COLLECTION: "North Island: Hokianga." LECTOTYPE (chosen here): Herb. T. Kirk, WELT 26175!

11. ***Carmichaelia australis*** var. ***egmontiana*** Cockayne et Allan, *Trans. & Proc. New Zealand Inst. 56*, 21 (1926). TYPE COLLECTION: "North Island: Egmont-Wanganui Botanical District - Common as a member of the subalpine scrub on Mount Egmont." LECTOTYPE (*fide* Allan 1961:383 as 224/145): *L. C. 1748*, WELT 654! ISOLECTOTYPE: WELT 647!

≡ *Carmichaelia egmontiana* (Cockayne et Allan) G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 255 (1945).

Notes: Simpson (1945) designated Cockayne's "1748" as the type specimens, numbering them 224/145 and 224/146; he did not select a specific sheet as the lectotype.

12. ***Carmichaelia australis*** var. γ ***grandiflora*** Hook.f., *Fl. nov.-zel. 1*, 50 (1852). TYPE

COLLECTION: "Milford Sound, *Lyall.*" LECTOTYPE (*fide* Allan 1961:378): *Lyall*, K left and right-hand pieces, labelled (1) and (2) (photocopy seen).

≡ *Carmichaelia grandiflora* (Hook.f.) Hook.f., *Handb. N. Zeal. fl.*, 49 (1864).

13. ***Carmichaelia australis*** var. β ***nana*** Hook.f., *Fl. nov.-zel. 1*, 50 (1852). TYPE COLLECTION: "Dry and mountainous country at the base of Tongariro, *Colenso.*" LECTOTYPE (chosen here): *Colenso 1156*, K top right piece, labelled (1) (photograph seen). ISOLECTOTYPES: WELT 26783!, 26784!

≡ *Carmichaelia nana* (Hook.f.) Hook.f., *Handb. N. Zeal. fl.*, 49 (1864).

Notes: The lectotype closely matches the description provided by Hooker (1864), and is labelled in Colenso's hand "1156 *Carmichaelia nana* n.sp. W.C." The number 1156 corresponds with a list of plants sent by Colenso to W. J. Hooker in September 1847: "1156. *Carmichaelia nana*, (M.S.) W.C., n. sp." (A copy of the list is held at CHR).

Also on the lectotype sheet is a second Colenso collection numbered "2380 *Carmichaelia nana.*" This corresponds with "2380. *Carmichaelia nana*, (vide, 1156) - in flower!" in a list of plants sent by Colenso to W. J. Hooker in June 1850. No locality is given. Hooker (1864) did not include this specimen in his description for *C. australis* var. *nana* as he makes no reference to flowers, and he does not refer to it in the protologue. This specimen has been redetermined by A. W. Purdie as *C. corrugata.* Three other collections on the lectotype sheet are labelled as *C. nana*, but these too have been redetermined as *C. corrugata* and *C. monroi* by A. W. Purdie.

In Herb. W. Colenso are two sheets (WELT 24218, 24219) labelled in Cheeseman's hand "*Carmichaelia nana* no locality probably near Tongariro." These are similar to the lectotype and are considered to be isolectotypes.

14. ***Carmichaelia australis*** var. ***strictissima*** Kirk, *Stud. fl. New Zealand*, 110 (1899). TYPE COLLECTION: "White Cliffs, Taranaki, *Cheeseman!*" LECTOTYPE (chosen here): *T. F. C.*, WELT 26223! ISOLECTOTYPES: AK 214595!, 4855!, WELT 26222!

15. ***Carmichaelia compacta*** Petrie, *Trans. & Proc. New Zealand Inst. 17*, 272-273

(1885). TYPE COLLECTION: "Kawarau Gorge and Dunstan Gorge, Clutha River, Otago." LECTOTYPE (*fide* Simpson 1945 as 224/490a): Dunstan Gorge, *D. Petrie*, WELT 53661! ISOLECTOTYPES: AK 4929!, 211346!, WELT 26306!

≡ *Huttonella compacta* (Petrie) Kirk, *Stud. fl. New Zealand*, 115 (1899).

16. ***Carmichaelia compacta*** var. ***procumbens*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 281 (1945). TYPE COLLECTION: "Rock and sandstone faces near Alexandra, Central Otago ... No. 456." LECTOTYPE (chosen here): *Simpson 456*, CHR 45904B! flowering piece, labelled (1). ISOLECTOTYPE: WELT 79541! LECTOPARATYPES: CHR 45904B-C!, WELT 79541!

Notes: Specimens with number 456 are mounted on three sheets and include flowers collected in "Dec 1938" and fruit collected in "early Feb 1939." Allan (1961:394) selected CHR 45904B as the type, but this includes pieces collected on two different dates. I reject Allan's typification, and a further lectotypification is necessary.

17. ***Carmichaelia corrugata*** Colenso, *Trans. & Proc. New Zealand Inst. 15*, 320-321 (1883). TYPE COLLECTION: "Dry stony plains Renwicktown, near Blenheim, South Island; *Mr. F. Reader.*" LECTOTYPE (chosen here): scrap specimen only: from Blenheim, *Colenso*, Herb. T. Kirk, WELT 36259! ISOLECTOTYPE: K (photograph and photocopy seen).

Notes: Allan (1961:391) indicated that the type was at WELT, but no specimen with precisely the details he gave has been located, and he may have merely been repeating the protologue.

Only a single Colenso specimen (WELT 32259) from the Blenheim area has been located, and this is in the Kirk herbarium. A single sheet (WELT 24220) in the Colenso herbarium contains a few seeds, and a specimen at K labelled "Com. W. Colenso, New Zealand, Sept./1883" was received the year *C. corrugata* was described. All these specimens are labelled as *Carmichaelia corrugata*, but none has a direct connection to Renwicktown or Mr. F. Reader.

However, part of the description reads "pod ... corrugated on one suture (mostly

the lower) with 8-9 thick closely formed wrinkles." This feature is not typical of *C. corrugata* but is clearly evident on WELT 36259 and the Colenso specimen at K; these specimens are consequently selected as lectotype and isolectotype.

18. ***Carmichaelia corymbosa*** Colenso, *Trans. & Proc. New Zealand Inst. 21*, 80 (1889). TYPE COLLECTION: "On the banks of streamlets, woods south of Dannevirke, County of Waipawa; 1887-88, flowering in January: *W. C.*" LECTOTYPE (chosen here): *Rev. W. Colenso*, WELT 26333! ISOLECTOTYPE: WELT 26334!

≡ *Carmichaelia flagelliformis* var. *corymbosa* (Colenso) Kirk, *Stud. fl. New Zealand*, 114 (1899).

Notes: Allan (1961:384) indicated that the type was at WELT, but he did not select one of the two sheets in the Kirk herbarium. No specimens were found in the Colenso herbarium, and Kirk (1899) acknowledges that he received his pieces from Colenso. Kirk (1899) indicates that other Colenso specimens were examined by N. E. Brown at Kew, but these have not been located.

19. ***Carmichaelia crassicaulis*** Hook.f., *Handb. N. Zeal. fl.*, 48-49 (1864). TYPE COLLECTION: "Middle Island; Mount Torlesse range, alt. 3500 to 5000 ft., and old moraines round Lake Ohau, *Haast*; Otago, Lindis Pass, *Hector and Buchanan.*" LECTOTYPE (chosen here): *Haast 83*, old moraines round Lake Ohau, December, K lower right hand flowering piece labelled (1) (photograph seen). LECTOPARATYPES: *Haast 61*, Lake Ohau; *Hector & Buchanan*, Otago, 1863; *Sinclair & Haast*, Prov. Canterbury, 1860-61; all on the lectotype sheet at K (photograph seen).

≡ *Corallospartium crassicaule* (Hook.f.) J.B.Armstr., *Trans. & Proc. New Zealand Inst. 13*, 333 (1881).

20. ***Carmichaelia cunninghamii*** Raoul, *Choix pl. Nouv.-Zél.*, 29, t. 28B (1846). TYPE COLLECTION: Not stated. LECTOTYPE (chosen here): illustration 28B, *Choix pl. Nouv.-Zél.* (1846).

21. ***Carmichaelia curta*** Petrie, *Trans. & Proc. New Zealand Inst. 25*, 271-272 (1893). TYPE COLLECTION: "Waitaki River, at Duntroon and Kurow. Flowering and fruiting pieces were gathered in the month of March." LECTOTYPE (chosen here): Duntroon, *D. Petrie*, AK 4930! ISOLECTOTYPE: AK 209770! LECTOPARATYPES: WELT 26706!

≡ *Huttonella curta* (Petrie) Kirk, *Stud. fl. New Zealand,* 116 (1899).

Notes: Simpson (1945) selected a sheet numbered 224/510 (WELT 53660) as the type; these pieces were collected during April 1892. I reject Simpson's typification, as the protologue gives the collection date as "the month of March." This date corresponds with AK 4930 and AK 209770, collected by Petrie from Duntroon, which I have chosen as the lectotype and isolectotype respectively. A specimen from the Petrie herbarium labelled "Kurow" (WELT 26706) is accepted as a lectoparatype.

22. ***Carmichaelia curta*** var. ***glabra*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 282 (1945). TYPE COLLECTION: "near Waitaki Dam - No. 97." LECTOTYPE (*fide* Allan 1961:395): *G. Simpson 97, J. S. Thomson, & H. H. Allan*, CHR 45906A! ISOLECTOTYPES: AK 103182!, CHR 45906B-C!, WELT 79540! LECTOPARATYPES: CHR 213010!, 213026!

Notes: Simpson (1945) also applied the number 97 to cultivated specimens, labelling them as "cotype." These are considered to be lectoparatypes.

23. ***Carmichaelia diffusa*** Petrie, *Trans. & Proc. New Zealand Inst. 25*, 272 (1893). TYPE COLLECTION: "East coast of Otago, near the mouth of the Otepopo River." LECTOTYPE (chosen here): *D. Petrie*, WELT 26152A! right-hand flowering piece, labelled (1). ISOLECTOTYPE: K (photograph seen). LECTOPARATYPES: WELT 26151!, K (photograph seen).

Notes: The type sheet for *C. diffusa* consists of two *Carmichaelia* taxa: the right-hand flowering piece is selected as the lectotype, and the left-hand fruiting piece is referable to *Carmichaelia robusta*. Both pieces are consistent with the description for *C. diffusa*. A very similar flowering piece in the Petrie herbarium (WELT 26151) from "Otepopo

Waitaki Co." is consistent with the description and protologue and is considered to be a lectoparatype. WELT 26152 and AK 4874 and 209776 are fruiting pieces from the type suite, but I do not select them as isolectotypes as they belong to *Carmichaelia robusta.*

"Otepopo River" is an older name of the Waianakarua River.

24. ***Carmichaelia enysii*** Kirk, *Gard. Chron., n.s., 21*, 512 (1884). TYPE COLLECTION: "South Island. Terraces of the river Porter, Canterbury, 2500 feet. *J. D. Enys and T. Kirk.*" LECTOTYPE (chosen here): Herb. T. Kirk, WELT 716! top centre piece, labelled "TYPE" and (1). LECTOPARATYPES: WELT 716 (2)!, (3)!, and (4)!, 26483!, 26484!

Notes: Simpson (1945) chose specimens from the Kirk herbarium (WELT 716; Simpson number 224/9) as the type. However, this sheet has three labels, all with different collection localities, and two of which have different dates - Jan 1882 and Jan 1883. These dates are prior to the publication of *C. enysii* in 1884, so Kirk is certain to have examined at least some of these pieces in preparing his description. The protologue gives the locality as "terraces of the river Porter, Canterbury, 2,500 feet. J. D. Enys and T. Kirk.", but specimens with this altitude and J. D. Enys as a collector have not been located.

A piece on Simpson's type sheet, WELT 716 top centre, matches the description in the protologue (Kirk 1884a) and the illustration in Kirk (1884b), which was intended as the original publication. This specimen has been labelled as the type by J. Macken on 12 Jan 1953, and I designate it as the lectotype.

There are nine other pieces on the sheet to which the lectotype specimen is attached, but to which labels these pieces refer is also not known. One piece is in flower (7), which contradicts the description and is probably a later collection, perhaps corresponding to the piece and undated label referring to Trelissick (8). The branchlets of this flowering piece are very similar to specimens 5, 6, and 9, and these could all be from the one collection. Specimens 2, 3, and 4 are similar to the lectotype, but because of the uncertainty as to their provenance they are treated as lectoparatypes.

Three other sheets in the Kirk herbarium are from the Porter River area, and two of these dated "Jan 1883" are also chosen as lectoparatypes.

C. enysii Kirk was effectively published on 19 April 1884, and is here accepted as the authority for *C. enysii*. However, Kirk (1884b) is often cited as the authority (see

Allan 1961:390), and indeed was probably intended by Kirk to be the original publication, but it was published one month later, in May 1884.

25. ***Carmichaelia enysii*** var. ***ambigua*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 269-270 (1945). TYPE COLLECTION: "No. 134 - from gravelly ground near Kurow, Waitaki Valley, North Otago." LECTOTYPE (*fide* Allan 1961:390): *Simpson 134*, CHR 45778A! ISOLECTOTYPES: AK 103141!, WELT 79539!

26. ***Carmichaelia fieldii*** Cockayne, *Trans. & Proc. New Zealand Inst. 50*, 163-64 (1918). TYPE COLLECTION: "South Island: North-western Botanical District ... wind-swept sandstone ledge on a small island ... Westhaven (West Wanganui). *W. H. Field & B. C. Aston*!" HOLOTYPE: *W. H. Field*, WELT 26317! (*fide* Simpson 1945 and Allan 1961:396, as number 224/588). ISOTYPES: WELT 8172!, 26315!, 26316!

Notes: Cockayne annotated WELT 26317 as the type sheet, and I accept this as the holotype. WELT 8172 from Oliver's herbarium, WELT 26316 from the B. C. Aston herbarium, and WELT 26315 were collected by B. C. Aston and are accepted as isotypes. Aston accompanied W. H. Field on his visit to West Wanganui Inlet when the specimens were collected (Cockayne 1917).

27. ***Carmichaelia flagelliformis*** Benth., in J. D. Hooker, *Fl. nov.-zel. 1*, 51 (1852). TYPE COLLECTION: "Northern and Middle Islands. East coast, *Bidwill, Colenso, Sinclair.* Akaroa, *Raoul.*" LECTOTYPE (*fide* Allan 1961:383): *W. Colenso 209*, 1847, K (photograph seen). LECTOPARATYPE: *W. C. 1517*, K (photograph seen).

Notes: Bentham alone is given as the authority, as he is cited by Hooker (1852, p. 51) as providing the name and description (ICBN Article 46.2).

28. ***Carmichaelia floribunda*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 283 (1945). TYPE COLLECTION: "Upcot Saddle, 1916." HOLOTYPE: *B. C. A.*, WELT 26709! ISOTYPES: WELT 26708!, 8185!

Notes: *C. floribunda* was described by Simpson (1945) from specimens collected by B.

C. Aston from Upcot Saddle, Marlborough in Feb 1916, and tentatively identified by him as *C. diffusa*. Simpson (1945) indicated that the type specimens at the Dominion Museum herbarium (WELT) were numbered 224/246 and 224/248. Simpson annotated these two sheets and was very specific in that he chose 224/246 (WELT 26709) as "type" and 224/248 (WELT 26708) as "co-type." I accept these as the holotype and isotype. WELT 8185 from the Oliver herbarium was also collected by B. C. Aston from Upcot Saddle in Feb 1916, and as it is almost certainly part of the original collection it is accepted as an isotype.

29. ***Carmichaelia glabrata*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 243-244 (1945). TYPE COLLECTION: "No. 263 ... from the Pelorus River." LECTOTYPE (chosen here): *G. Simpson 263*, CHR 45709A! flowering pieces, labelled (1) and (2). ISOLECTOTYPES: AK 209771!, CHR 45709B-E!, WELT 79538! LECTOPARATYPES: AK 209771!, CHR 45709A-E!, WELT 79538!

Notes: Allan (1961:380) selected CHR 45709A as the type. This sheet has flowering pieces collected from the Pelorus River bridge during Jan 1937, and fruit from a cultivated plant, presumably collected on a later date. For this reason I reject Allan's typification, and a further lectotypification is necessary.

30. ***Carmichaelia gracilis*** J.B.Armstr., *Trans. & Proc. New Zealand Inst. 13*, 336 (1881). TYPE COLLECTION: "Site of the city of Christchurch." LECTOTYPE (chosen here): *J. B. A.*, CHBG 6116! (held at CHR).

Notes: A sheet in Herb. T. Kirk (WELT 26738) is labelled "By the Avon Chch coll. J. B. Armstr. Dr von Haast." A smaller, and possibly original label reads "Carmichaelia sp nov Avon." This plant material could be considered a lectoparatype if it could be established that it was available to Armstrong when he described *C. gracilis*.

31. ***Carmichaelia grandiflora*** var. ***alba*** Kirk, *Stud. fl. New Zealand*, 111 (1899). TYPE COLLECTION: "Near the Waimakariri glaciers, *Enys and Kirk*. Jan." LECTOTYPE (chosen here): *T. Kirk*, WELT 686! ISOLECTOTYPES: WELT 687!, 26444!; *Kirk 1148*, K (photocopy seen).

Notes: The sheets chosen as lectotype and isolectotypes were originally labelled in Kirk's hand as "Carmichaelia grandiflora var. robusta." Kirk further annotated the lectotype sheet as "var. albida," but apart from this the labels are consistent with the protologue. The unpublished epithet "albida" differs from the published *alba*.

32. ***Carmichaelia grandiflora*** var. ***divaricata*** Kirk, *Stud. fl. New Zealand*, 111 (1899). TYPE COLLECTION: "South Island: Mount White and valley of the Poulter, 2,300ft., *Enys*! Near Greymouth, Westland, *Helms*! Jan." LECTOTYPE (chosen here): Mount White, *J. D. Enys*, WELT 26554! LECTOPARATYPE: K (photocopy seen).

≡ *C. divaricata* (Kirk) Cockayne, *New Zealand plants and their story*, ed. 3, 163 (1927).

Notes: WELT 26524 has two labels with one piece, but to which label the single piece belongs is not clear. The top label reads "near Greymouth, R. Helms", and the bottom label "Hokitika Mr Tipler." If it could be established that the single piece belonged with the Helms label this piece would be treated as a lectoparatype.

33. ***Carmichaelia grandiflora*** var. ***dumosa*** Kirk, *Stud. fl. New Zealand*, 111 (1899). TYPE COLLECTION: "Broken River basin." LECTOTYPE (chosen here): *T. Kirk*, WELT 688! LECTOPARATYPES: AK 4897!, WELT 689!

Notes: The sheet selected as the lectotype is from the Trelissick Basin. This is an alternative name for the Broken River Basin, Castle Hill, and Prebble Hill areas, Canterbury.

34. ***Carmichaelia hollowayi*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 277 (1945). TYPE COLLECTION: "from the foothills of Mt. St. Mary - No. 88." LECTOTYPE (chosen here): *G. Simpson 88*, CHR 45804! pieces labelled (1), (2), (3), (4), and (5). ISOLECTOTYPES: AK 103186!, 103187! LECTOPARATYPES: CHR 213032!, 213048!

Notes: Allan (1961:393) chose CHR 45804 as the type. This sheet includes flowers

collected during Jan 1937 and fruits collected from a cultivated plant, presumably at a later date. The fruits are not typical of *C. hollowayi* as they have inflated rather than flattened valves; they belong to *C. monroi*. Accordingly they are excluded from being type material. The necessary lectotypification is made above.

35. ***Carmichaelia hookeri*** Kirk, *Stud. fl. New Zealand*, 115 (1899). TYPE COLLECTION: "North Island: east coast, from the Akiteo River southwards; South Makara Stream; Plimmerton; Pencarrow, Wellington, *T. K.* Dec., Jan." LECTOTYPE (*fide* Allan 1961:386): South Makara Stream, *T. Kirk 847*, WELT 26241! LECTOPARATYPES: WELT 26231-26234!, 26237!, 26242!, 26257!, 44174!

≡ *C. flagelliformis* var. *hookeri* (Kirk) Cheeseman, *Man. New Zealand fl.*, 116 (1906).

Notes: Although the lectotype and lectoparatype WELT 26242 are very similar flowering pieces I am not certain that they are from the same collection. Kirk has numbered them 847 and 848, which suggests that they are different collections, and only the lectotype is dated "Jan. 1 1880."

36. ***Carmichaelia juncea*** Hook.f., *Fl. nov.-zel. 1*, 51 (1852). TYPE COLLECTION: "Northern and Middle Islands. East Cape, *Sinclair*. Hawkes' Bay and Taupo, *Colenso*. Akaroa, *Raoul*." LECTOTYPE (chosen here): *Colenso 2038*, WELT 24247!

Notes: The protologue lists collections by Sinclair, Colenso, and Raoul. The Sinclair collection has not been located, and that of Raoul is referable to *Carmichaelia robusta*. Colenso's specimens came from Hawke's Bay and Taupo.

In a list of plants that Colenso sent to W. J. Hooker is reference to two specimens (nos. 1845 and 2938) labelled "*Carmichaelia juncoides*." Number 1845 is described as a "small new sp., plains near Mission Station Hawkes Bay; grows in beds!", and number 2038 (WELT 24247) is a "fruiting specimen" with a note "see no. 1845." WELT 24247 is selected as the lectotype as it has Colenso's original handwritten number "2038" attached to the specimen, and it is consistent with Hooker's description and protologue.

Several sheets are probable paratypes, but this cannot be confirmed with certainty. In the Colenso herbarium are four sheets (WELT 24249, 24250, 24251, 24252) labelled

"*Carmichaelia juncea* Col. no locality." In addition, the Petrie herbarium contains a flowering piece (WELT 26702) labelled "*C. juncea* Hawks Bay ex Herb W. Colenso," and the Cheeseman herbarium contains a sheet (AK 4932) with a flowering and a fruiting piece; these were probably all taken from the original Colenso suite of specimens.

37. ***Carmichaelia juncea*** var. γ ***parviflora*** Benth., in J. D. Hooker, *Fl. nov.-zel. 1*, 51 (1852). TYPE COLLECTION: Not stated. TYPE SPECIMEN: Not located.

Notes: At Kew herbarium Colenso's collection "3796 *Carmichaelia minimiflora* n.sp. W.C." has been relabelled twice. Firstly as *Carmichaelia juncea* Col., and later with var. *parviflora* Hook.f. appended to this. The collection comprises two specimens, but it cannot be established with certainty that these are the ones seen by Bentham. The name is treated as *nomen dubium.*

Bentham alone is given as the authority, as he is cited by Hooker (1852:51) as providing the name and description (ICBN Article 46.2).

38. ***Carmichaelia kirkii*** Hook.f., *Hooker's Icon. Pl. 14*, t. 1332 (1881). TYPE COLLECTION: "New Zealand: Otago, prov., in the Cardrona Valley, *T. Kirk*; Otepopo, *D. Petrie*." LECTOTYPE (*fide* Allan 1961:390): Cardrona Valley, *T. K. 726*, K lower two pieces, labelled (1) and (2) (photocopy seen). ISOLECTOTYPES: WELT 26731!, 26732!, 26737!, 44061! LECTOPARATYPES: AK 4876!, 4877!, 209786!, K (photocopy seen), WELT 26733!, 26735A- B!, 26736!

Notes: Allan (1961:390) designated Kirk 726 as the type. This collection comprises two pieces which were received at Kew on "6/77." One of these is in fruit, and compares well with similar pieces in the Herb. T. Kirk at WELT, which I have selected as isolectotypes. In addition, WELT 26732 is dated 8/1/77, which is six months earlier than the receipt of similar pieces at Kew.

At the top of the lectotype sheet are three flowering pieces and a note by Kirk which acknowledges that "these from Otepopo were collected by Mr Petrie." A suite of similar flowering specimens at WELT and AK are either from, or in, the Herb. D. Petrie, and I consider these to be lectoparatypes. Some fruiting pieces collected by

Petrie are not considered to be lectoparatypes (e.g., AK 209785! and 4877!).

Simpson (1945) accepted the Cardrona collection as the type, but did not select a specific sheet from among those available. He did however suggest that Kirk 835 (224/259) is a "co-type." Hooker (1881) gave the origin and collector as "Otapopo, M. Petrie," but I have amended this to Otepopo and D. Petrie.

39. ***Carmichaelia kirkii*** var. ***strigosa*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 267 (1945). TYPE COLLECTION: "from the terraces of the Poulter River, Upper Waimakariri Basin ... 112 type." LECTOTYPE (chosen here): *G. Simpson 112 & W. B. Brockie*, CHR 45771A! flowering piece, labelled (1). ISOLECTOTYPES: AK 103151!, CHR 45771C-D!, 213042A-B!, WELT 79537! LECTOPARATYPES: AK 103150!, CHR 45771A!, C-D!, 213042A-B!, WELT 79537!

Notes: Allan (1961:390) chose CHR 45771A as the type. This sheet comprises a flowering piece and a fruiting piece collected at different times. The dates are not given on the type sheet with the number CHR 45771, but rather on CHR 213042A and B. The flowering pieces were collected from a plant cultivated at Dunedin during Dec 1939 and the fruiting pieces during Feb 1940. I reject Allan's typification, and a further lectotypification is necessary.

40. ***Carmichaelia lacustris*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 282-283 (1945). TYPE COLLECTION: "Grassy edges and stoney shores of Lake Te Anau and Lake Manapouri ... type specimens from shores below the Accomodation House, L. Manapouri, No. 445." LECTOTYPE (chosen here): *G. Simpson 445 & J. S. Thomson*, CHR 45810A! left-hand upper and lower pieces, labelled (1) and (2). ISOLECTOTYPES: CHR 45810B!, WELT 79536! LECTOPARATYPES: AK 103181!, CHR 45810A-B!, 213056!, 213059!, 213060!, WELT 79536!

Notes: Allan (1961:395) selected CHR 45810A as the type. This sheet comprises pieces collected from the wild and flowering and fruiting pieces from cultivated plants (Fig. 2.1). The only date given is Feb 1939, and this is likely to be the date that the wild collection was made.

In the protologue Simpson states "In the type habitat the branches are short and

stiffly erect ... in cultivation they are often longer and procumbent, with only the tips ascending." The lectotype pieces correspond with the description of plants from the wild in having upright branchlets; the long, procumbent flowering and fruiting pieces would be from cultivated plants.

41. ***Carmichaelia micrantha*** Colenso, *Trans. & Proc. New Zealand Inst. 26*, 313 (1894). TYPE COLLECTION: "Edges of forest, head of Rangitikei River, County of East Taupo; *Mr. Patrick Stirling McLean*: 1893." LECTOTYPE (chosen here): *P. S. McLean*, WELT 24238! ISOLECTOTYPE: K (photograph seen).

42. ***Carmichaelia monroi*** Hook.f., *Handb. N. Zeal. fl.*, 49 (1864). TYPE COLLECTION: "Middle Island: from halfway up to the summit of Macrae's Run, *Munro*." LECTOTYPE (*fide* Allan 1961:393): *Dr. Monro*, K! lower three pieces, labelled (1), (2), (3).

Notes: The specific epithet *monroi* commemorates Sir David Monro (1813–1877), who sent specimens of this plant to J. D. Hooker. Hooker (1864) published the specific epithet as *munroi* which is an orthographic error for *monroi* (ICBN Art. 60.1 Ex. 3). Subsequent authors have corrected the spelling (e.g., Kirk 1896, 1899; Cheeseman 1906).

43. ***Carmichaelia monroi*** var. ***longecarinata*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 279 (1945). TYPE COLLECTION: "No. 94 ... from terraces above the Poulter River, Upper Waimakariri River Basin, Canterbury." LECTOTYPE (*fide* Allan 1961:394): *G. Simpson 94*, CHR 45807B! ISOLECTOTYPE: WELT 79535! LECTOPARATYPES: AK 103183!, CHR 213053!, 213055!, 213057!

Notes: Collection number 94 comprises three separate dates: Dec 1936 (CHR 213053, 213055, 213057); Jan 1938 (AK 103183); and Xmas 1938. Simpson's (1945) protologue states "Type specimen No. 94 ex author's herbarium in the Herbarium Plant Research Bureau, Wellington." This collection was made during Christmas 1938 and comprises two sheets, with CHR 45807B selected as the type by Allan (1961:394). This sheet is labelled in Simpson's hand "type specimens [*Carmichaelia*] *monroi* var. *longecarinata* nov."

The other number 94 collections were almost certainly examined by Simpson, and are therefore lectoparatypes.

44. ***Carmichaelia muelleriana*** Regel, *Gartenflora 36*, 611-612 (1887). TYPE COLLECTION: "Wahrscheinlich stammt dieselbe aus Neu-Seeland" (probably originated out of New Zealand). TYPE SPECIMEN: Not located.

Notes: As a type specimen cannot be found, this name is treated as *nomen dubium.*

45. ***Carmichaelia multicaulis*** Colenso, *Trans. & Proc. New Zealand Inst. 25*, 329 (1893). TYPE COLLECTION: "Open grassy flats in gullies south of Dannevirke, County of Waipawa; 1889-92: *W. C.*" LECTOTYPE (chosen here): *W. C.*, WELT 24236! ISOLECTOTYPES: WELT 24237!, 26331!, K (photograph seen).

46. ***Carmichaelia nigrans*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 285-286 (1945). TYPE COLLECTION: "Flood bed margins at the Makarora R., L. Wanaka ... No. 244 ... collected by *L. W. McCaskill.*" LECTOTYPE (*fide* Allan 1961:369): *L. W. McCaskill*, CHR 45814C! ISOLECTOTYPES: AK 103180!, 209773!, CHR 45814A-B!, WELT 79534! LECTOPARATYPES: CHR 45815!, B-H!

Notes: The lectoparatypes are numbered Simpson 159 and are "cultivated from cutting from TYPE plant 45814 [Simpson 244]." Another four sheets (CHR 213062A-B!, 213063!, 213064!) from cultivated plants are also labelled with number 244, but the collection dates of "flowers Dec. 1946 fruits Feb. 1947" post-date the publication of *C. nigrans.*

47. ***Carmichaelia nigrans*** var. ***tenuis*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 286 (1945). TYPE COLLECTION: "Old flood beds at the Waiho and Cook Rivers, Westland ... No. 155." LECTOTYPE (*fide* Allan 1961:369): *P. Graham & M. Bradley*, CHR 45816B! ISOLECTOTYPES: AK 209772!, WELT 79533!

48. ***Carmichaelia odorata*** Benth., in J. D. Hooker, *Fl. nov.-zel. 1*, 50 (1852). TYPE COLLECTION: "Northern Island. East coast, *Colenso.*" LECTOTYPE (*fide* Allan

1961:380): *Colenso 942*, 1849, K (photocopy seen). LECTOPARATYPES: 50 *Carmichaelia*, 1847, K top and bottom left-hand pieces (photocopy seen); *Colenso 50B*, 1844, K top right-hand piece (photocopy seen); *Colenso 1043*, 1849, K (two sheets; photocopies seen).

Notes: WELT 24224 and 24226 from the Colenso herbarium are possible syntypes, but as the labels give no collection details this cannot be confirmed.

Bentham alone is given as the authority, as he is cited by Hooker (1852:50) as providing the name and description (ICBN Article 46.2).

49. ***Carmichaelia orbiculata*** Colenso, *Trans. & Proc. New Zealand Inst. 22*, 459-460 (1890). TYPE COLLECTION: "Desert of Rangipo, near Mount Tongariro, County of East Taupo; 1889: *Mr. H. Hill.*" LECTOTYPE (chosen here): *H. Hill*, WELT 24216! ISOLECTOTYPE: WELT 26459!

≡ *C. enysii* var. *orbiculata* (Colenso) Kirk, *Stud. fl. New Zealand*, 108 (1899).

Notes: Allan (1961:391) gave the type as "W, H. Hill, 1889," but a dated sheet has not been located at WELT. Allan was probably citing an abbreviated version of the protologue. The Colenso herbarium sheet chosen as the lectotype is not dated, but is from Rangipo and was collected by H. Hill.

In the Petrie herbarium is a sheet (WELT 26459) labelled "*Carmichaelia* orbiculatis (aris): Col. = *C. enysii* var. *orbiculata,*" with a note in Petrie's hand "This is a piece of the type specimen from Colenso's Herb. D.P." This piece is selected as an isolectotype.

50. ***Carmichaelia ovata*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 260 (1945). TYPE COLLECTION: "No. 269 ... from the Awatere Valley, near Seddon, Marlborough." LECTOTYPE (*fide* Allan 1961:386): *G. Simpson (269) & J. S. Thomson*, CHR 45564A! ISOLECTOTYPES: AK 102883!, 102884!, CHR 45564C-E!, WELT 79532!

Notes: Although the lectotype sheet comprises flowering and fruiting pieces, it cannot

be established with certainty that these were collected at different times, as was Simpson's practice in preparing type specimens. Allan's typification is therefore accepted.

Examination of *C. ovata* collections at CHR indicates that during February it is possible to collect both flowering and fruiting pieces in Marlborough.

51. ***Carmichaelia paludosa*** Cockayne, *Trans. & Proc. New Zealand Inst. 47*, 113 (1915). TYPE COLLECTION: "South Island: Westland - Abundant in lowland swamps. *L. C.*" LECTOTYPE (here chosen): *L. C. 1743*, WELT 26649! ISOLECTOTYPE: WELT 26648! LECTOPARATYPE: WELT 26574!

Notes: The lectotype and isolectotype were collected by Cockayne from the type locality. The lectoparatype was collected by "Miss Annie Gunn from near Wataroa," and as it bears Cockayne's collection number 1743 he almost certainly had it available when he prepared the description for *C. paludosa.*

52. ***Carmichaelia petriei*** Kirk, *Stud. fl. New Zealand*, 111 (1899). TYPE COLLECTION: "South Island: Otago: Clutha Valley; north of Clyde; valleys and terraces on east and west of the Dunstan mountains; *Petrie!*" LECTOTYPE (*fide* Allan 1961:388): Dunstan Gorge, *D. Petrie*, WELT 26194! LECTOPARATYPES: AK 4865!, WELT 26109!, 26193!, 26195!

53. ***Carmichaelia petriei*** var. ***minor*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 271-272 (1945). TYPE COLLECTION: "No. 556 ... from flats at the Matukituki River near the forks to east and west." LECTOTYPE (chosen here): *Geo. S. 556*, CHR 45748A! flowering piece, labelled (1). ISOLECTOTYPE: WELT 79531! LECTOPARATYPES: CHR 45748A!, 213070-213072!, WELT 79531!

Notes: Allan (1961:388) selected CHR 45748A as the type. This sheet comprises flowering pieces collected in Jan 1938 and fruiting pieces collected at Easter 1939. Because of these different collection dates I reject Allan's typification, and a further lectotypification is necessary.

54. ***Carmichaelia pilosa*** Benth., in J. D. Hooker, *Fl. nov.-zel. 1*, 50-51 (1852). TYPE COLLECTION: "Northern Island. East coast, *Colenso.*" LECTOTYPE (chosen here): *Colenso 1971*, K (photocopy seen).

≡ *C. odorata* Benth. var. *pilosa* (Benth.) Kirk, *Stud. fl. New Zealand*, 113 (1899).

Notes: Bentham alone is given as the authority, as he is cited by Hooker (1852:51) as providing the name and description (ICBN Article 46.2).

55. ***Carmichaelia prona*** Kirk, *Trans. & Proc. New Zealand Inst. 27*, 350 (1895). TYPE COLLECTION: "South Island: Lake Lyndon; 2,800ft.: *J. D. Enys and T. Kirk.*" LECTOTYPE (chosen here): *T. Kirk*, WELT 26294! ISOLECTOTYPES: WELT 26287!, 26293!, 26298!, 29658!

≡ *Huttonella prona* (Kirk) Kirk, *Stud. fl. New* Zealand 116 (1899).

Notes: Allan (1961:396) indicated the type was in the Kirk herbarium at WELT and was annotated "Lake Lyndon, 2800 ft., J. D. Enys and T. Kirk." A label with exactly this annotation has not been located, and it is likely that Allan was merely citing the protologue. I have chosen WELT 26294 as the lectotype as it is from Lake Lyndon at an altitude of 2800 ft. This sheet is dated "Jan. 1883", a feature shared with the isolectotypes, and thus indicating single collection.

No labels mention J. D. Enys as a collector, and only the lectotype gives the altitude of 2800 ft. WELT 26297 from "Lake Lyndon" is probably a paratype, as it is similar to the type pieces, but it makes no reference to a date or altitude.

56. ***Carmichaelia ramosa*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 272 (1945). TYPE COLLECTION: "No. 474 ... from the northern slopes of Dansy's Pass, North Otago." LECTOTYPE (*fide* Allan 1961:389): *G. Simpson 474*, CHR 45809C! ISOLECTOTYPES: AK 70628!, CHR 45809B!, WELT 79530!

Notes: A note in Simpson's hand on AK 70628 is dated 28/1/1939, whereas the sheets at CHR are dated 28/1/1938. All the pieces are similar, and it appears that there is a

transcription error on one of the sheets.

Simpson (1945) also indicated that number 556 is a "type," but he did not do this in his usual manner, as it is merely included among his list of specimens. No specimens with this number have been found.

57. ***Carmichaelia rivulata*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 264-265 (1945). TYPE COLLECTION: "No. 105 ... from old river bed of the Dobson River, above L. Ohau." LECTOTYPE (chosen here): *G. Simpson 105*, CHR 45572A! flowering pieces, labelled (1) and (2). ISOLECTOTYPES: AK 70624!, CHR 45572B-C!, WELT 79529! LECTOPARATYPES: AK 70624!, CHR 45572A-C!, 213082!

Notes: Allan (1961:387) selected CHR 45572A as the type. This sheet comprises flowering pieces collected on 21 Dec 1937 and fruiting pieces collected in March 1938. Because of these different collection dates I reject Allan's typification, and a further lectotypification is necessary.

58. ***Carmichaelia robusta*** Kirk, *Stud. fl. New Zealand*, 111 (1899). TYPE COLLECTION: "South Island: Broken River Basin, 2,000ft. to 2,800ft., *Enys* and *T. K.* Dec., Jan." LECTOTYPE (*fide* Simpson 1945 as 224/560): *T. Kirk 741*, WELT 26750! ISOLECTOTYPES: *Kirk 1140*, K. LECTOPARATYPES: AK 4868!; *Kirk 1140*, K; WELT 26752-26756!, 26760!

≡ *C. petriei* var. *robusta* (Kirk) Cheeseman, *Man. New Zealand fl.*, 113 (1906).

Notes: The fruiting piece selected as lectotype by Simpson bears the Kirk number 741, and the label indicates that Kirk sent duplicates to Kew as number 1140. WELT 26760 is a flowering piece numbered Kirk 744, and with a note that 1140 has been sent to Kew. Thus, two pieces were sent to K with the number 1140, but only the fruiting piece is an isolectotype.

A suite of specimens in Herb. T. Kirk from the Broken River basin is treated as lectoparatypes. Kirk (1899) indicates that Enys collected some of the original specimens. However, his name does not appear on any of the Broken River collections, but is on several from the adjacent Castle Hill (e.g., WELT 26783-26786). These would

have been available to Kirk when he prepared his description for *C. robusta*, and he may have included Castle Hill in the general area of the Broken River basin. These too could be considered lectoparatypes.

59. ***Carmichaelia silvatica*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 251 (1945). TYPE COLLECTION: "No. 130 ... from a plant in cultivation, collected by Mr. A. D. McKinnon at the Waipoua River." LECTOTYPE (chosen here): *Mr. A. D. McKinnon*, CHR 45558A! fruiting pieces. ISOLECTOTYPES: AK 103110!, WELT 79528! LECTOPARATYPES: AK 103110!, CHR 45558A!

Notes: Allan (1961:382) selected CHR 45558A as the type. This sheet comprises flowering and fruiting pieces which were almost certainly collected on two different dates. For this reason I reject Allan's typification, and a further lectotypification is necessary.

60. ***Carmichaelia solandri*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 253-254 (1945). TYPE COLLECTION: "No. 324 ... from a plant in cultivation collected at Whakatane by Miss L. B. Moore." NEOTYPE (chosen here): from plant in cultivation collected by Miss L. B. Moore from Whakatane, *G. Simpson 324*, March 1948, CHR 195572A! fruiting piece. ISONEOTYPES: CHR 195572B-C!, WELT 79527!

Notes: Simpson (1945) indicated that the type specimens were "in the Herbarium Plant Research Bureau, Wellington" (now CHR). Allan (1961) could not find these. In October 1969 four sheets with Simpson's number 324 were received at CHR. These comprise flowering and fruiting pieces which were collected "Nov.10/47" and "March 12 1948" respectively. The labels in Simpson's hand correspond with the protologue. In the absence of a collection pre-dating the publication of *C. solandri*, I select a neotype from among these.

61. ***Carmichaelia stricta*** C.B.Lehm., *Hamburger Garten- Blumenzeitung 8*, 372 (1852). TYPE COLLECTION: Not stated. LECTOTYPE (chosen here): *E. Otto*, Gartenzeitung, 1852, S (photocopy seen).

Notes: The label on the lectotype sheet is written in Lehmann's hand (B. Nordenstam, pers. comm. June 1994).

62. ***Carmichaelia subulata*** Kirk, *Stud. fl. New Zealand*, 112-113 (1899). TYPE COLLECTION: "South Island: Marlborough: Whakamarina, Blenheim, *T. K.* Nelson: Cheviot, *Haast!* Canterbury: Burnham, Lincoln, Akaroa, &c., *T. K.* Broken River, *Enys and T. K.* Otago, *Buchanan!* Sea-level to 2,000ft. Dec., Jan." LECTOTYPE (chosen here): Lincoln, *T. Kirk*, Dec 16 1881, Herb. T. Kirk 796, WELT 26749! LECTOPARATYPES: WELT 26135!, 26147!, 26626-26629!, 26631!, 26770!, 26771!

63. ***Carmichaelia suteri*** Colenso, *Trans. & Proc. New Zealand Inst. 23*, 383 (1891). TYPE COLLECTION: "South Island, `near Mount Cook Hermitage, alt. 2,540ft.!; creeping upwards over stones amongst tussocks:' *Mr. H. Suter*, in lit., 1890." LECTOTYPE (*fide* Allan 1961:392): Herb. W. Colenso, WELT 24217! ISOLECTOTYPE: WELT 26466!

≡ *C. uniflora* var. *suteri* (Colenso) G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 275 (1945).

Notes: Three other H. Suter collections from the Hermitage and Hooker Valley (WELT 26463!, 26472A-B!) are not considered to be part of the original collection, as their labels do not fully agree with the protologue.

64. ***Carmichaelia uniflora*** Buchanan, *Trans. & Proc. New Zealand Inst. 16*, 395 (1884). TYPE COLLECTION: "not uncommon in the Waitaki Valley." LECTOTYPE (chosen here): Buchanan herbarium, WELT!

Notes: Only a single collection of *C. uniflora* has been located in the Buchanan herbarium at WELT, and this is chosen as the lectotype. No collection locality is given. Buchanan (1884) gives the distribution as "not uncommon in the Waitaki Valley," so presumably his collection comes from there.

65. ***Carmichaelia uniflora*** Kirk, *Gard. Chron., n.s., 21*, 512 (1884). TYPE COLLECTION: "South Island, New Zealand, Valley of the Poulter, Canterbury. *J. D. Enys.*" NEOTYPE

(chosen here): Poulter River, Upper Waimakariri River Basin, Canterbury, Grassland on lower flat terrace, *G. Simpson & W. B. Brockie*, Jan. 1938, CHR 45805!

Notes: Allan (1961:392) noted that the type could not be found. Several collections made by T. Kirk and J. D. Enys from the general area of the type locality have been examined, but none is exactly consistent with the locality, description, and protologue. Three sheets are from the Grassmere area (AK 4823!, WELT 26465!, 26468!) and one is from the mountains above the Waimakariri (K!). The neotype selected was collected from the type locality at the Poulter River.

C. uniflora Kirk was effectively published on 19 April 1884 (Kirk 1884a), one month earlier than Kirk (1884b), which was probably intended to be the original publication.

66. ***Carmichaelia violacea*** Kirk, *Stud. fl. New Zealand*, 112 (1899). TYPE COLLECTION: "South Island: Coleridge Pass, 2,500ft. to 3,000ft., *Enys and T. K.* Jan." LECTOTYPE (*fide* Simpson 1945:265; Allan 1961:388): *T. Kirk*, WELT 26279! ISOLECTOTYPES: *Kirk 1146*, K; WELT 26276!, 26277!, 26278!

67. ***Carmichaelia virgata*** Kirk, *Stud. fl. New Zealand*, 112 (1899). TYPE COLLECTION: South Island: Otago, *Petrie!* Makarewa and Orepuke, Southland, *T. K.* Dec., Jan." LECTOTYPE (*fide* Allan 1961:389): Orepuke, *T. Kirk*, WELT 26119! ISOLECTOTYPE: WELT 26123!, AK 4873!, 209787!

Notes: The two sheets from Herb. T. Cheeseman at AK were collected by Petrie and sent to Cheeseman via Kirk. Although their locality is given as Otago they are very similar to the lectotype and isolectotype, and I consider them to be part of the Southland collection.

68. ***Carmichaelia williamsii*** Kirk, *Trans. & Proc. New Zealand Inst. 12*, 394 (1880). TYPE COLLECTION: "North Island: Raukokore Bay, Bay of Plenty, Hicks' Bay - *Archdeacon W. L. Williams.*" LECTOTYPE (*fide* Allan 1961:381): Raukokere, Bay of Plenty, *W. L. Williams*, 1879, Herb. T. Kirk, WELT 26354! LECTOPARATYPES: AK 4841!, 209794!

Notes: There are another six sheets at WELT and one at AK collected by "W.L.W." These are not consistent with the description, protologue, or date of publication, and are not considered to be type material. The pieces have leaves or pods, which contradicts the description, they are from a different locality, or the date given is after the species was described.

2.5 TYPIFICATION OF NAMES IN *CHORDOSPARTIUM*

Chordospartium **Cheeseman,** *Trans. & Proc. New Zealand Inst. 43*, 175 (1911)
TYPE SPECIES: *C. stevensonii* Cheeseman.
TYPE COLLECTION: See 2 below.

1. ***Chordospartium muritai*** A.W.Purdie, *New Zealand J. Bot. 23*, 157-161 (1985).
TYPE LOCALITY: Clifford Bay, Marlborough. HOLOTYPE: *A. W. Purdie*, CHR 415452!
ISOTYPE: CHR 415453!

2. ***Chordospartium stevensonii*** Cheeseman, *Trans. & Proc. New Zealand Inst. 43*, 175 (1911). TYPE COLLECTION: "South Island: Foothills of the Seaward Kaikoura Mountains, near the mouth of the Clarence River; altitude, 1,500-2,500 ft.; *Mr. George Stevenson!*" LECTOTYPE (chosen here): New Genus of Leguminosae. Clarence Bridge, *G. Stevenson*, March 1910, AK 210743! fruiting pieces. ISOLECTOTYPE: AK 4948!
LECTOPARATYPES: AK 4947!, 210739-210742!; K (photograph seen).

Notes: The protologue reads "I have to express my obligations to Mr. Stevenson for ... both flowering and fruiting pieces. Most of these were obtained from a tree growing near his house ... The flowering season stretches from the middle of November to the end of December, and the fruit is ripe at the beginning of April." There are seven sheets in the Cheeseman herbarium which comprise flowering and/or fruiting pieces. As indicated by the flowering and fruiting times given by Cheeseman, these would have likely been collected at different times.

The lectotype sheet (AK 201743) comprises two fruiting pieces, and has a handwritten label "New Genus of Leguminosae. Clarence Bridge G. Stevenson March 1910" and a tag with "No. 1." This collection is part of a suite originally numbered AK

4948/1, 2, 3, and 4, and which have subsequently been renumbered as AK 4948, 210741, 210742, 210743. AK 4948 comprises two fruiting pieces and is an isolectotype, but AK 210741 and 210742 are flowering pieces and are lectoparatypes. Another three sheets at AK and one at K appear to represent a different collection, as the label reads "Waiautoa (Clarence Bridge) Marlborough," and the specimens were used to illustrate the species by Cheeseman (1914); these too are selected as lectoparatypes.

2.6 TYPIFICATION OF NAMES IN *CORALLOSPARTIUM*

Corallospartium **J.B.Armstr.**, *Trans. & Proc. New Zealand Inst. 13*, 333-334 (1881)
TYPE SPECIES: *C. crassicaule* (Hook.f.) J.B.Armstr., loc. cit. ≡ *Carmichaelia crassicaulis* Hook.f.
TYPE COLLECTION: See under *Carmichaelia crassicaulis*.

1. ***Corallospartium crassicaule*** var. ***racemosum*** Kirk, *Stud. fl. New Zealand*, 107 (1899). TYPE COLLECTION: "Otago: near the Lindis Pass, *Buchanan!*" LECTOTYPE (*fide* Allan 1961:371): Herb. Buchanan, WELT! ISOLECTOTYPE: Lindis Pass, Otago, *J. Buchanan*, AK 4815!

≡ *Corallospartium racemosum* (Kirk) Cockayne et Allan, *Trans. & Proc. New Zealand Inst. 57*, 50 (1926).

2.7 TYPIFICATION OF NAMES IN *NOTOSPARTIUM*

Notospartium **Hook.f.**, *Hooker's J. Bot. Kew Gard. Misc. 9*, 176, t. 3 (1857)
TYPE SPECIES: *N. carmichaeliae* Hook.f.
TYPE COLLECTION: See 1 below.

1. ***Notospartium carmichaeliae*** Hook.f., *Hooker's J. Bot. Kew Gard. Misc. 9*, 176, t. 3 (1857). TYPE COLLECTION: "Montibus insulae mediae Novae-Zelandiae ad flumen Waihopai *Dom. Munro* invenit florentem Dec. 1853, et prope Canterbury *D. Waites.*" LECTOTYPE (*fide* Allan 1961:372): banks of the Waihopai in sandy and rocky places, N. Zeland, *Dr. Munro*, Xmas 1853, K (photocopy seen).

Notes: The material collected by Waites from Canterbury (K, photocopy seen) belongs to *N. torulosum*. Accordingly, it is excluded from being type material of *N. carmichaeliae*.

2. ***Notospartium glabrescens*** Petrie, *Trans. & Proc. New Zealand Inst. 53*, 366-367 (1921). TYPE COLLECTION: "Awatere Valley, Marlborough: *T. Kirk!* Mouth of Clarence River: *G. Stevenson!* Throughout the upper basin of the Clarence River and its tributary valleys: *B. C. Aston!*" LECTOTYPE (chosen here): near mouth of Clarence River, Marlbro., *Geo. Stevenson*, 1914, WELT 26868! LECTOPARATYPES: Herb. D. Petrie, WELT 26831!, 26863!, 26864!, 26866!, 26869-26873!, 26877A-B!, 26880-26883!; Herb. B. C. Aston, WELT 26823-26826!, 54238!, 54240A!

Notes: Allan (1961:372) indicated that the type was at WELT but did not specify a particular sheet from those available. A second lectotypification is therefore needed.

The collection dates and localities, and the condition and nature of plant material from the Herb. B. C. Aston correspond with sheets in the Herb. D. Petrie. This indicates that, for many of his collections, Aston sent Petrie some pieces and kept others for his own herbarium. Therefore, the sheets selected as lectoparatypes from Herb. D. Petrie correspond with the lectoparatype sheets from the Herb. B. C. Aston. The only difference is that labels on the Aston sheets give the name as *Notospartium torulosum*, whereas Petrie has crossed this out and renamed them as *N. glabrescens*.

There are an additional 12 sheets at WELT from the Herb. B. C. Aston collected in 1915 and 1916 from the Clarence River basin. As their dates do not correspond exactly with specimens from the Herb. D. Petrie they are not considered to be syntype material.

The Kirk specimens from the Awatere Valley have not been located. However, there are four sheets from the Herb. T. Kirk at WELT labelled *N. carmichaeliae* and collected from various parts of the Awatere River valley.

3. ***Notospartium torulosum*** Kirk, *Stud. fl. New Zealand*, 117 (1899). TYPE COLLECTION: "South Island: Nelson and Canterbury: gorge of the Mason River, Amuri, *Haast! Rev. F. H. Spencer! S. D. Barker! L. Cockayne!* Waikari, *S. D. Barker!* Ravines at the base of Mount Peel, *W. E. Barker!*" LECTOTYPE (*fide* Allan 1961:372): Mason

River, Amuri, *Sir Julius von Haast*, Herb. T. Kirk, WELT 26796! LECTOPARATYPES: WELT 26802!, 26862A! and B!, 43533!, 44183!, 44184!

CHAPTER THREE

TAXONOMY OF *CARMICHAELIA* AND *NOTOSPARTIUM*

3.1 INTRODUCTION

The procedure for a formal taxonomic revision follows an ordered series of activities, during the course of which the taxonomy of the group being studied progressively develops, finally culminating in a new and/or revised classification. The following is an outline, stage by stage, of the typical process for the revision of a genus (adapted from Davis & Heywood 1963).

Stage 1: Scope the problem. The genus to be studied is defined and the relevant literature on it gathered. Important literature includes the protologue for all published names, previous flora treatments or revisions, and specific information such as that on reproductive biology, palynology, or wood anatomy. It is important to determine the approximate number of species and their distribution.

Stage 2: Plant material. Firstly, it is necessary to obtain the type material for each name, and specimens that belong to the genus should be loaned from other herbaria. Field observations and collections, and experimental garden studies should begin. At this stage a large amount of field work is often necessary.

Stage 3: Character identification and assessment. Study individual specimens and select qualitative characters and/or quantitative characters which show discontinuities or variation within the genus. Data can be assembled in tables, as working descriptions, or notes and sketches. A complete list of characters is compiled as this ensures all plant parts are examined.

Stage 4: Group individuals. Specimens that share similar characters are grouped together.

Stage 5: Character testing. Thoroughly test all characters that support particular groups. This stage often involves examining a single character across all specimens.

Stage 6: Character variation. Study variation in characters that show incomplete separation between the groups, and any other patterns of variation that occur within groups. This may provide characters that further support groups established at stage 4.

Stage 7: Distribution and ecology. Map the distribution of the groups, seeking ecological and geographical patterns.

Stage 8: Classification. Decide how the groups will ranked and named. Define what specific or infraspecific concepts and criteria will be used, and apply these consistently to the group. It is often necessary at this stage to consult other treatments of the genus, or family to which the genus belongs, to be consistent across the whole group.

Stage 9: Write the revision. Correctly apply names to particular taxa, prepare formal descriptions, provide distributional and habitat information.

The above summary is a guide and there will be situations when it cannot be followed from one stage to another. Depending on the genus being revised each stage will have a different degree of emphasis. For example, in the present revision of *Notospartium* particular emphasis is given to stage 7, distribution and ecology. Furthermore, there will be a certain amount of backtracking as specimens and characters have to be reexamined or more material gathered.

In the formal revision for *Carmichaelia* information for each species is presented under a series of headings: description, distribution and habitats, recognition, variation, representative specimens, etymology, illustrations, conservation status, and discussion. This format allows for a large amount of information on each species to be presented and easily located. This format has developed only recently in New Zealand for monographic revisions (e.g., *Heliohebe*, Garnock-Jones 1993), but similar formats have been used for new species descriptions for some time (e.g., *Asplenium chathamense*, Brownsey 1985; *Chordospartium muritai*, Purdie 1985).

3.2 MATERIALS AND METHODS

3.2.1 *Carmichaelia*

The taxonomic revision presented here is based on the study of *Carmichaelia* in the field, herbarium, and experimental garden. Extensive field work was undertaken throughout New Zealand, and herbarium specimens were deposited in CHR. Sites were often visited several times to assess flower and fruit characteristics. Herbarium material for study was obtained from AK, AKU, BM, CANU, CHR, K, NZFRI, OTA, and WELT.

Fresh plant material from the field and experimental garden, some of which was preserved in FAA, was used for the character assessment, evaluation, and determination of states. When character states were defined and their distribution among the taxa understood, formal descriptions were prepared from herbarium and freshly collected or preserved wild collected plant material. Herbarium material was of limited value for floral descriptions as the floral parts discolour and they are often squashed beyond recognition or reconstruction. Floral descriptions were prepared from fresh material and/or material preserved in FAA. Vegetative and fruit characters were examined in either herbarium or freshly collected wild or cultivated material.

Standardised descriptions are provided as this allows for comparison between species, which has not been possible with original descriptions, and those of Hooker (1864), Kirk (1899), Cheeseman (1906, 1925), Simpson (1945), and Allan (1961). A complete description was usually prepared for each taxon, however, to be consistent in the designation of some character states it was often necessary to examine a single character across all taxa.

To assess whether the variation observed for particular characters in different species of *Carmichaelia* had a genetic basis or whether it was due to phenotypic variation, a number of plants were raised from seed and cuttings and grown under uniform conditions at the Landcare Research experimental garden, Lincoln. Large shrubby species of *Carmichaelia* were cultivated in open ground plots and the smaller dwarf shrub species were grown in potting bags in a bark based potting mix with slow release fertiliser. All plants were grown outside. Only general comparisons were made between the original wild collection and subsequent cultivated plants, and no data was gathered that allowed statistical analyses to be undertaken.

Plants from several populations of *Carmichaelia australis* were scored to assess

variation in stem diameter, pod length, and pod width between different populations, and plant variation within populations. The raw data is presented in Appendix 1. The statistical methods used were analysis of variation (ANOVA and nested ANOVA) and the Multiple Comparison Scheffe test with confidence limits of 95%. These statistical methods are available in S-Plus (Statistical Sciences Inc., 1998). Five measurements of stem diameter, pod length, and pod width were taken from each of 243 plants from 13 populations of *C. australis*. Nine of the populations were from Canterbury and four from the North Island. Variation within each population was analysed by summarising the individual measurements for each plant, and inter-population variation was analysed by summarising the mean measurements for each population. The nested ANOVA model was used on the complete data set to examine plant variation within populations.

3.2.2 *Notospartium*

The taxonomic problem in *Notospartium* was resolved by field studies, and the examination of cultivated plants and herbarium material. Thorough examination was made of vegetative, floral, and fruit characters.

Field studies have been made in Marlborough at George Stream, lower Clarence River, Ure River, Woodside Creek, Medway River, Isis River, Upcot Saddle, Spray River, Avon River, and Waihopai River. Herbarium specimens at AK, CHR, and WELT have been examined, including important specimens from the Petrie Herbarium at WELT. A large collection of living plants up to 20 years old and of known wild origin have been available for study at the Landcare Research experimental nursery, Lincoln.

For the ecological part of the study rock and soil samples were collected from the field at the exact sites plants were growing. A semiquantitative chemical analysis of parent rock material using X-ray fluorescence was conducted by Spectra Chem Analytical, and a quick-test soil analysis was done by the Soil Fertility Service, Invermay.

3.3 CHARACTERS

Species of *Carmichaelia* are distinguished by different combinations of growth habit, cladode, floral, and fruit characters. Leaves occur on seedling and juvenile plants

but are generally absent on adult plants of all species and so are not able to be used for taxonomic purposes.

Growth habit among species of *Carmichaelia* varies considerably and includes small rhizomatous dwarf shrubs 3–5 cm high (e.g., *C. corrugata*), dwarf shrubs up to 20 cm high (e.g., *C. monroi*), prostrate shrubs (e.g., *C. appressa*), upright shrubs (e.g., *C. williamsii*), and a liana (*C. kirkii*). Although *C. corrugata* and *C. uniflora* are the only strictly rhizomatous species a number of others (e.g., *C. australis* and *C. curta*) often develop a rhizomatous habit, particularly when they have been browsed. The dwarf shrubs (e.g., *C. nana*) can also appear to be rhizomatous but this is a result of their short stems being buried underground.

Cladodes are the leafless shoots that occur on all species of *Carmichaelia*. The cladodes are the main photosynthetic structures on the plant, lines of stomata run parallel to their length, they are usually smooth or with weak striations, and they lack grooves. Their diagnostic attributes include length, width, thickness, shape in transverse section, and colour. The polymorphic quantitative characters vary continuously within *Carmichaelia*, although some species, or groups of species, generally have a particular range of variation. For example, the cladodes in transverse section are compressed (*C. williamsii*), plano-convex (e.g., *C. hollowayi*; some forms of *C. monroi*), and terete (*C. kirkii*). *Carmichaelia corrugata*, *C. nana*, and *C. uniflora* are very similar in having narrow, short, and generally flattened cladodes, and they also have a considerable range of variation (Fig. 3.4).

The usefulness of cladodes for providing taxonomic characters is unfortunately limited by the general similarity of a number of species, considerable intraspecific variation, and the virtually continuous variation that occurs in *Carmichaelia*. Nevertheless, the taxonomic value of cladodes was given considerable importance by Simpson (1945), who I consider over-emphasised their value. Simpson placed particular emphasis on their width and used this as an important character in his recognition of a number of species in his subgenus *Carmichaeliella*. In the dichotomous key for this subgenus the use of cladode diameter is clearly seen as an important character. My experience with this key is that the natural variation that occurs in a single population is often so great that several species can often be keyed out using cladode characters.

The inflorescences in *Carmichaelia* are racemose, lateral, usually only one per

node, upright, spreading or drooping, and the flowers 1-many. The flowers of *Carmichaelia* are zygomorphic and hermaphrodite, and comprise four petals (1 standard petal, 2 wing petals, 1 fused keel petal), a campanulate calyx with 5 short lobes, and diadelphous stamens. The stamens and gynoecium are enclosed within the keel petal. One species, *C. williamsii*, differs from all other species of *Carmichaelia* in having large (>15 mm long) yellow flowers. Among the other species with smaller (<12 mm long) white flowers and coloured floral guides, two main groups can be recognised by differences in the wing and keel petals. For example, in *C. australis* the wing petals are longer than the keel petal and the keel petal is less than 4.5 mm long. In comparison, in *C. monroi* the wing petals are shorter than the keel petal and the keel petal is greater than 8.5 mm long.

Floral characters are constant and uniform for particular species and I consider that they generally provide more reliable taxonomic characters than vegetative characters. The main floral characters of taxonomic importance are the size and shape of the standard, keel, and wing petals, the wing and keel petal length ratio, the shape of the keel petal, and the calyx lobes. Several new floral characters have been identified, including for *C. compacta*, *C. curta*, and *C. juncea* variation in the degree of fusing of the ventral filaments, and for *C. vexillata* the position of the standard petal in relation to the keel length.

The base colour of the flowers is usually white although most species have purple blotches or veins. The purple colour often varies considerably in intensity and tone within and between species and is therefore of limited taxonomic use. There are some exceptions to the general pattern of flower colour: in *C. corrugata* and *C. uniflora* the abaxial surface of the standard is green, *C. williamsii* differs from all other species in having large yellow petals, and *C. arborea* usually has white petals with only occasionally a pale central blotch.

The fruits of *Carmichaelia* are woody, have a replum to which the valves are attached, lack an intruded suture, and the style remnant forms a prominent and usually pungent beak. Differences occur in fruit size, shape, dehiscence, and orientation, and each of these characters is of taxonomic significance. Fruit length varies continuously from *C. juncea* (3.5 mm) to *C. williamsii* (34 mm) with all species having a specific range of variation. The fruit are two main shapes, with most species being laterally compressed, but those of subgenus *Huttonella* are dorsiventrally compressed. The

valves and replum are typically elliptic, oblong, or oblanceolate, and the woody beak positioned on the upper surface usually gives the pod a slightly falcate shape. The dehiscence of the valves varies considerably, some species are indehiscent and others partially or totally dehiscent. Species such as *C. compacta* and *C. monroi*, and their close relatives, are indehiscent, with the valves not detaching at all, whereas in *C. australis* and *C. appressa* the valves are completely dehiscent. *Carmichaelia corrugata* and *C. uniflora* are usually indehiscent, but may sometimes be slightly dehiscent only at the base. Partial dehiscence of the valves occurs in a number of different ways. For example, in *C. arborea* and *C. odorata* the valves are dehiscent at the apex and hinged at base, and in *C. kirkii* and *C. enysii* they are hinged at the side. The fruit of most species are usually oriented in a spreading, upright, or slightly drooping manner, although in *C. arborea* and *C. odorata* they are always erect.

The fruit have traditionally been regarded as providing important taxonomic characters at species rank, and distinct types are characteristic of Simpson's (1945) subgenera. Although the pod types are characteristic of Simpson's subgenera, it is often difficult to recognise a particular species by only the pod as closely related species are generally very similar. For example, the pods of *C. monroi* and *C. vexillata* are alike, and virtually impossible to separate. There is also often a considerable amount of intraspecific variation in pod shape and/or size in some species, as is seen in the widespread *C. juncea* and *C. australis*.

Seeds of all species of *Carmichaelia* are reniform, oblong or elliptic-oblong, and they lack a strophiole. Some species are quite uniform in size, shape and colour, but for others there is sometimes considerable variation in these characters. For example: the seeds of *C. juncea* and *C. australis* vary a great deal in colour; those of *C. juncea* are uniformly small; and those of *C. kirkii* are off-white with black or dark purple mottling. Two species, *C. arborea* and *C. odorata,* have a thin and membranous testa, whereas all other species have a testa that is thick and hard.

The above discussion indicates that each of the main character types (e.g., growth habit, cladodes, flowers, and fruit) has some attribute that is particularly variable. Two general patterns of morphological variation have been identified for the species included in this revision. Firstly, those species with a wide distribution often have regional or local variability of one or several characters and this is usually constant for a given area. For example, branchlet size and shape of *C. corrugata, C. monroi, C. nana*, and *C.*

uniflora; pod size of *C. juncea*; pod shape of *C. nana*; and the growth habit of *C. monroi*. Secondly, species with a local or regional distribution are generally uniform, or if there is variation it is throughout the range of the species. For example, *C. astonii* has variable branchlet size throughout its distribution; *C. compacta* has variation in growth habit; and *C. curta* has variation in the hairiness of the calyces.

A simple and reliable method to assess whether character variation is due to phenotypic variation or if it has a genetic basis is to cultivate plants under uniform cultural conditions. This type of "common garden" experimental study is particularly suitable for morphological characters that exhibit variation in different geographic areas or in different habitats. The fundamental premise of this method is to grow plants gathered from different sites under uniform environmental conditions that are unaffected by any irregularities that would have occurred in different natural habitats. Collections of plants are normally made systematically from throughout the geographic and ecological ranges of the study taxon, and replicates should be taken to facilitate statistical analyses. Herbarium vouchers of wild plant material should be made at the time of collection, and these can be compared at a later date with cultivated specimens for the character(s) of interest. Statistical comparisons between cultivated and wild material can be made using ANOVA and multiple comparisons (e.g., Tukey's test).

An alternative method to common garden experiments for elucidating genetic and phenotypic components of variation is transplant experiments. This method uses clones or replicates and these are planted into a number of different environments. The effects of these different environments on plant material can be statistically evaluated.

Common garden and transplant studies can be analysed and interpreted in a number of ways. They can test hypotheses that different species may differ significantly for a given character, or that there is no difference between some species using a particular character. Alternatively, they can be used to test hypotheses that environmental conditions influence plant growth attributes.

Carmichaelia australis, a widespread and shrubby species, provides the most complex patterns of geographic and clinal variation in growth habit, cladode size and shape, pod size and shape, and seed colour. These characters were examined on fresh and herbarium material from throughout the range of the species, and they form either more or less continuous clines or predominantly occur in a specific geographic area. In a particular region or geographic area one or two characters may appear to be discrete,

but other characters are continuous and clinal with surrounding regions. Despite variation in four morphologically important and visually obvious characters *C. australis* has very uniform floral characters, and these are considered to be the uniting feature of a species that has previously been split into numerous geographically based taxa.

Analysis of variation (ANOVA) of stem diameter, pod length, and pod width for 13 populations of *C. australis* confirmed that there is significant interpopulation variation (Table 3.1; Fig. 3.1-3.3). Furthermore, the nested ANOVA demonstrated that there is significant variation of plants within populations, and this was confirmed for several populations by undertaking analysis of variation of plants within each population (Tables 3.1, 3.2). In the different Canterbury populations of *C. australis* there is overlap in pod length and width (Fig. 3.1, 3.2). Stem diameter is also variable, but separates into two main groups (Fig. 3.3). Inland populations from Lake Coleridge, Dry Stream, Lake Lyndon, Lake Lyndon Road, and Rakaia River have broader diameter stems than those populations from Banks Peninsula (Mt Cavendish, Lake Ellesmere, Lake Forsyth, and Akaroa). The North Island populations have wider pods than those from Canterbury, and the stem diameter for the Tongariro and Taumarunui populations are intermediate between the inland Canterbury and Banks Peninsula populations. The absence of population samples from throughout the range of *C. australis* prohibits any definitive conclusions being drawn from this study, but it is apparent that from the sample populations that variation occurs in different geographic areas.

Table 3.1 Comparison of character variation among several mostly Canterbury populations of *C. australis*. ** highly significant; *** very highly significant.

Character	ANOVA of plant summary data (*P*)	Nested ANOVA of raw data (*P*)
Stem - population	0***	1.12727e008***
- plant in population	-	3.17500e011***
Pod length - population	0***	0.003734406**
- plant in population	-	0.000000000***
Pod width - population	0***	0.0000227702***
- plant in population	-	0.0000000000***

Table 3.2 Comparison of plant variation within several mostly Canterbury populations of *C. australis* for stem diameter, pod length, and pod width. ANOVA: * significant at < 0.05 confidence level; ** very significant at < 0.01 confidence level; *** very highly significant at < 0.001.

Population	Grid reference	*n*	Stem diameter			Pod length			Pod width		
	(MS 260)		Mean±SD	*F* value	*P* =	Mean±SD	*F* value	*P* =	Mean±SD	*F* value	*P* =
Lake Lyndon	K35 04- 66-	7	2.73±0.16	2.49	0.1753	8.24±0.66	11.76	0.0186*	3.31±0.46	11.50	0.0194*
Dry Stream	K34 058 173	26	2.88±0.37	1.03	0.3188	8.01±1.23	0.01	0.9711	2.95±0.28	3.69	0.0663
Lake Coleridge	K35 96- 61-	24	2.72±0.31	0.41	0.5258	7.95±1.33	20.50	0.0002***	2.83±0.25	3.69	0.0678
Lake Lyndon Road	K35 02- 63-	22	2.63±0.44	2.76	0.1117	7.49±1.22	0.49	0.4914	3.11±0.28	0.01	0.9511
Rakaia River	K35 93- 54-	30	2.41±0.39	0.35	0.5550	7.74±1.21	0.95	0.3373	3.33±0.40	0.07	0.7880
Akaroa	N37 055 091	23	1.36±0.21	17.29	0.0004***	6.10±1.01	17.96	0.0004***	2.84±0.23	4.61	0.0434*
Lake Forsyth	M36 885 116	30	1.32±0.14	0.81	0.3751	5.58±0.77	0.09	0.7694	2.59±0.25	1.03	0.3179
Mt Cavendish	M36 876 357	22	1.82±0.21	2.18	0.1545	6.95±1.02	3.09	0.0936	2.80±0.33	2.32	0.1428
Lake Ellesmere	M36 795 166	25	1.6±0.23	11.64	0.0023**	6.72±0.83	0.71	0.4063	2.88±0.25	0.02	0.8855
Taumarunui	S18 06- 54-	8	1.36±0.18	0.96	0.3641	6.44±1.08	0.008	0.9316	4.06±0.61	0.001	0.9949
Manawatu	T24 49- 93-	7	1.37±0.19	2.31	0.1891	6.13±1.38	0.37	0.5683	3.59±0.26	0.40	0.5543
Tongariro	S20 31- 26-	16	2.12±0.28	0.97	0.3392	6.91±1.14	1.20	0.2915	3.39±0.36	12.82	0.0031**
Mt Taranaki	P20 92- 16-	3	2.30±0.37	0.05	0.8575	8.16±1.11	12.36	0.1763	4.37±0.64	0.14	0.7673

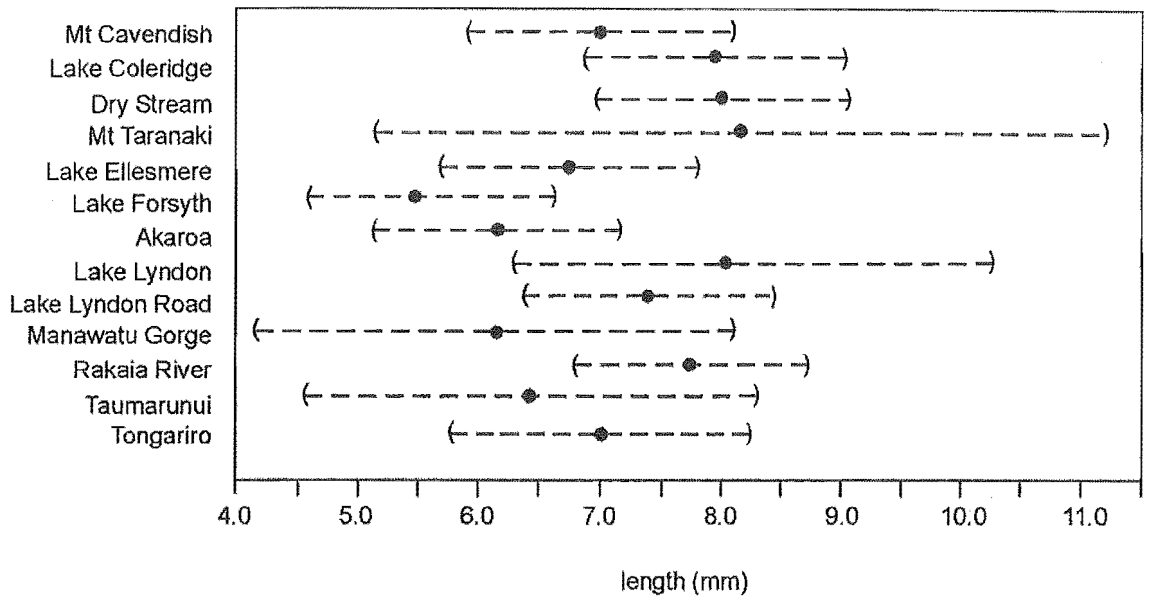


Fig. 3.1 Variation in pod length for populations of *Carmichaelia australis*. Confidence limits 95%.

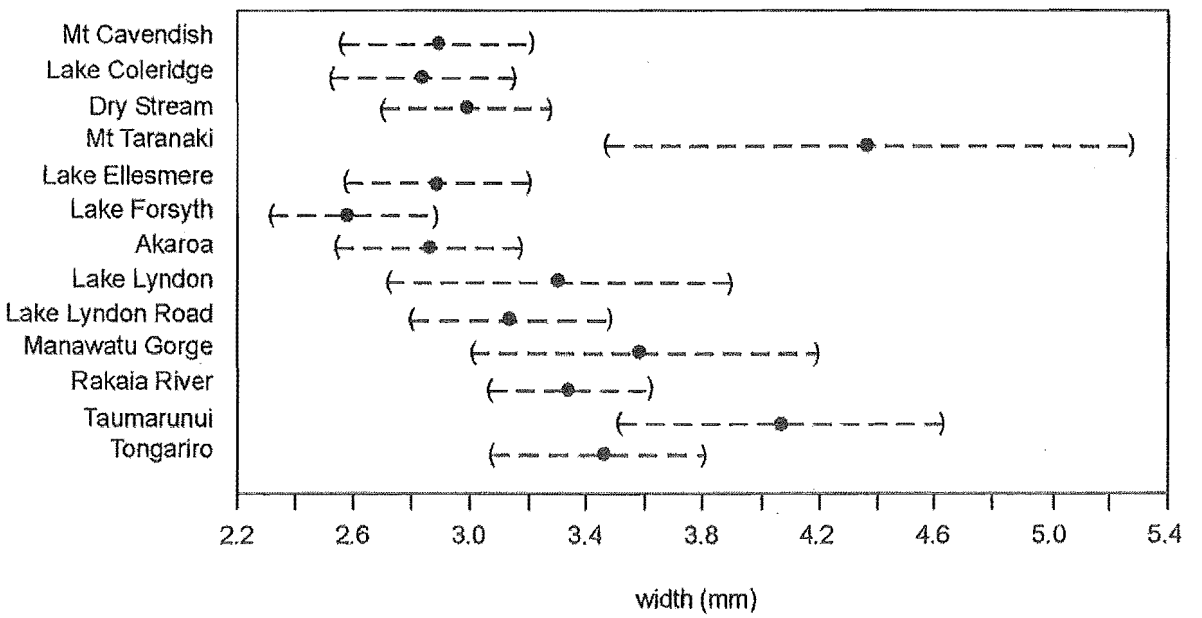


Fig. 3.2 Variation in pod width for populations of *Carmichaelia australis*. Confidence limits 95%.

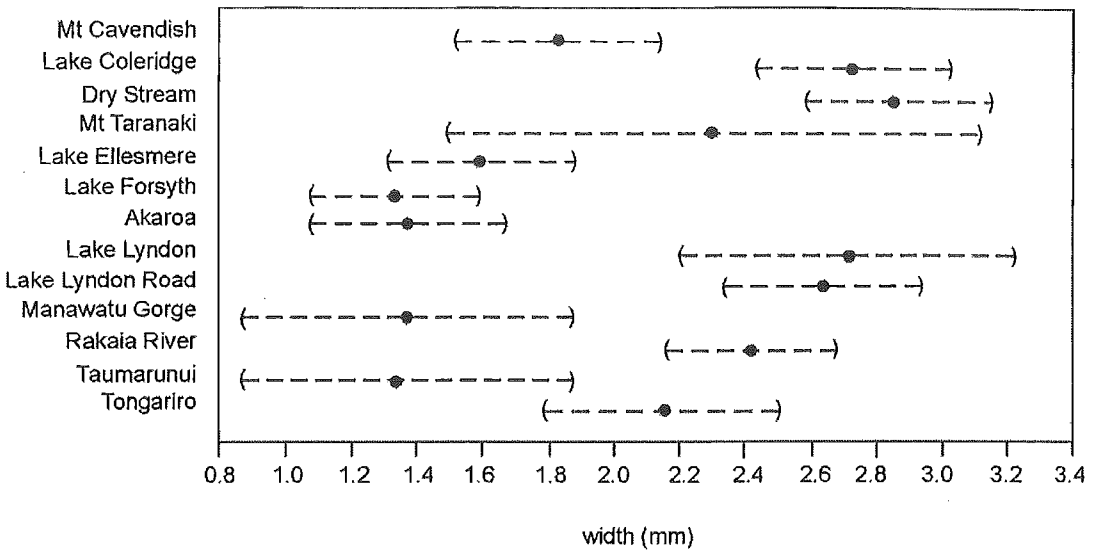


Fig. 3.3 Variation in cladode width for populations of *Carmichaelia australis*. Confidence limits 95%.

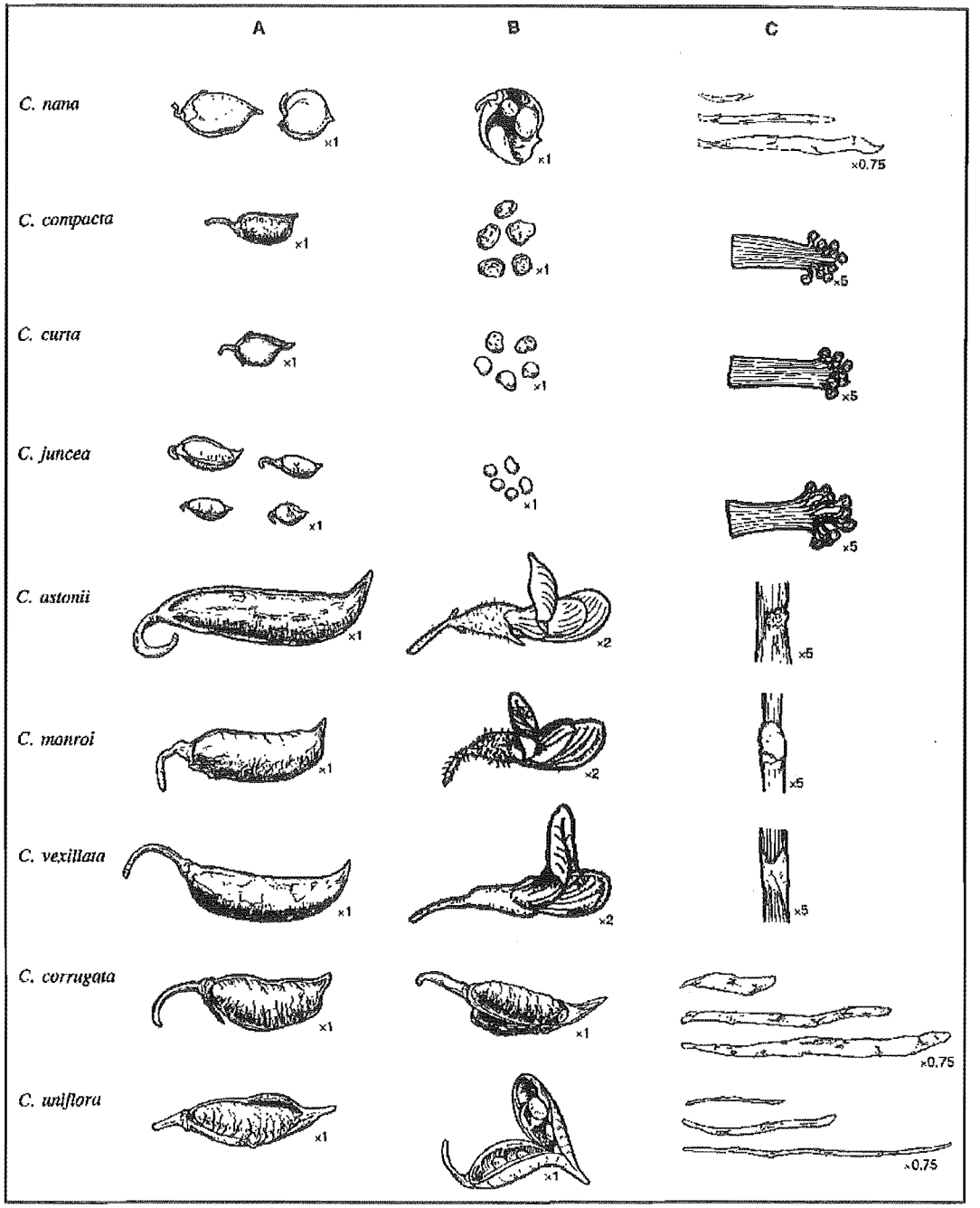


Fig. 3.4 Diagnostic characters. *Carmichaelia nana*, **A**, undehisced pods; **B**, dehisced; **C**, cladodes. *C. compacta*, **A**, pod; **B**, seeds; **C**, lower filament fusion. *C. curta*, **A**, pod; **B**, seeds; **C**, lower filament fusion. *C. juncea*, **A**, pods; **B**, seeds; **C**, lower filament fusion. *C. astonii*, **A**, pod; **B**, flower; **C**, stipule. *C. monroi*, **A**, pod; **B**, flower; **C**, stipule. *C. vexillata*, **A**, pod; **B**, flower; **C**, stipule. *C. corrugata*, **A**, indehiscent pod; **B**, dehiscent pod; **C**, cladodes. *C. uniflora*, **A**, indehiscent pod; **B**, dehiscent pod; **C**, cladodes.

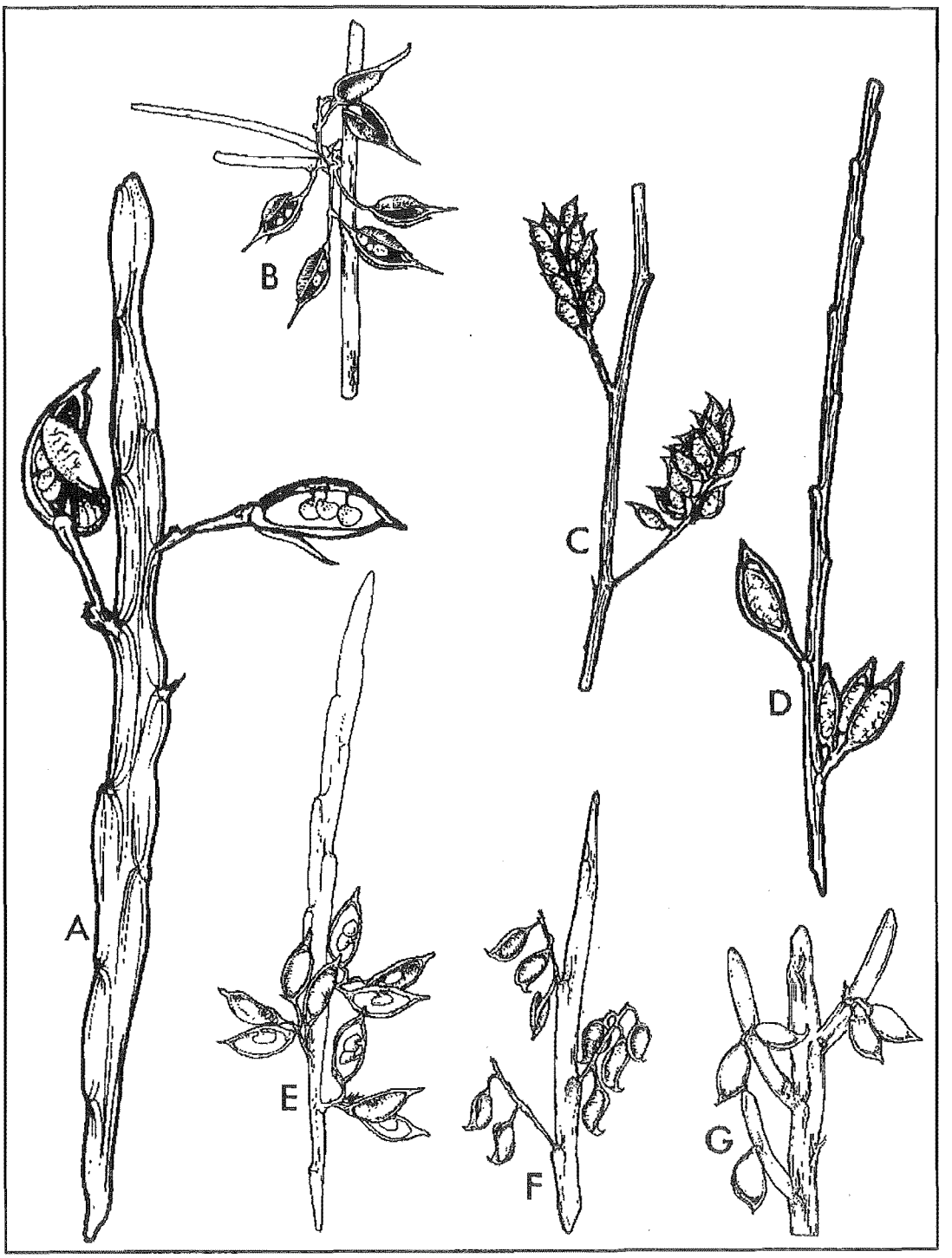


Fig. 3.5 Pod shape and orientation. **A**, *Carmichaelia williamsii*; **B**, *C. kirkii*; **C**, *C. odorata*; **D**, *C. arborea*; **E**, *C. australis*; **F**, *C. petriei*; **G**, *C. hollowayi*.

3.4 APPLICATION OF THE MORPHOLOGICAL SPECIES CONCEPT

As outlined in the introduction the recognition of some species of *Carmichaelia* has in the past been extremely difficult. For example, to identify and name some collections to a particular species, the geographic locality of the collection has often been the equal of any morphological character. Clearly, species concepts and the emphasis given to particular characters are major issues in the taxonomy and classification of species of *Carmichaelia*. The morphological species concept was adopted for this revision of *Carmichaelia* as it was considered that this should allow for a reliable, stable, and predictive classification to be developed that would allow names to be applied in the field and herbarium in a confident and assured manner.

To provide background for the application of the morphological species concept in the current revision it is necessary to review the species concepts that have been applied to earlier taxonomic work in *Carmichaelia*. Previous taxonomic treatments of *Carmichaelia*, including the recognition of new species, have been constrained by few and generally sparse collections. A result of this is that for a number of species of *Carmichaelia* the range of natural variation, the limits of variation, and the inter- and intra-specific relationships have been poorly understood. It is because of these factors that it has been extremely difficult for previous revisions to erect a reliable and robust classification and to provide adequate species circumscriptions — particularly in regard to the range of natural variation that is accepted. Furthermore, considerable emphasis has often been given to variation in cladode and pod sizes and shapes, often at the expense of floral characters. Although none of the earlier treatments of *Carmichaelia* explicitly adopt a species concept, Simpson's (1945) major revision of *Carmichaelia* is typical of some of the earlier taxonomic treatments. I therefore briefly discuss his classification and species concepts.

It is clear from reading Simpson's revision that he gave particular emphasis to pod characters at two levels within his classification. Firstly, he developed an infrageneric classification of eight subgenera for which many of the major differences were in pod characters, particularly the degree of valve dehiscence and pod orientation and persistence. For example, subgenus *Thomsoniella* differs from subgenus *Carmichaeliella* in the pods being erect (spreading in *Carmichaeliella*) and the valves

dehiscing apically and remaining closed at the base (valves completely separating in *Carmichaeliella*). A number of the subgenera appear to be distinct natural groups that have no obvious close relationship to other subgenera, and they usually include a number of closely related species (e.g., *Huttonella*). In contrast, other subgenera such as *Enysiella* are less distinct, have similarities to other subgenera (e.g., *Carmichaeliella*), and comprise only one or two species. Although Simpson did use some growth habit attributes in his subgeneric classification, to construct a more reliable and robust classification and to better understand the infrageneric relationships of *Carmichaelia* it is probably necessary to consider a number of other characters, particularly those of the flowers.

Secondly, at the rank of species Simpson mostly used differences in pod size and shape to distinguish species within many of his subgenera. Considerable emphasis was also given to branchlet diameter. This is well illustrated in subgenus *Carmichaeliella* where he recognised eighteen species with the main differences usually being variation in pod size and shape and branchlet diameter. The emphasis on these characters is seen at many of the couplets in his key to *Carmichaeliella* (Simpson 1945, p. 248). Unfortunately, the considerable emphasis given to pods and branchlets in Simpson's application of the morphological species concept has resulted in a classification that lacks robustness and stability and is therefore difficult to apply.

Simpson also recognised 11 varieties, with most of these being distinguished from the species in which they are included by differences in growth habit, branchlet diameter, and/or hair abundance. The character(s) used to distinguish most of the varieties are trivial and have usually been applied to only one part of the natural variation of a species. Most of the named varieties have some factor that makes their application difficult, and this was often acknowledged by Simpson (1945). For example, they may only be named and described from their type locality with little knowledge of their full distribution (e.g., *C. angustata* var. *pubescens*), others are stated to be difficult to distinguish from the species (e.g., *C. curta* var. *glabra*), and others are acknowledged as being a single part of a variable species (e.g., *C. kirkii* var. *strigosa*). The flaws with Simpson's classification at the rank of variety are that he has failed to apply the rank equally to all variants within a species, he has failed to apply the same criteria to all species of *Carmichaelia*, and he has over-complicated the classification by providing names that are usually very difficult and often impossible to apply. I believe

that Simpson has failed to recognise that variation is to be expected as a result of dealing with populations, and that variation is often a natural part of a species circumscription.

A strength of Simpson's revision is that he was able to recognise that the pods exhibited a great range of morphological variation, and after careful study and analysis he developed a hierarchical classification involving both subgenera and species. In using pod attributes for his subgeneric and species level classification Simpson has been very consistent in terms of separating the different pod characters for each classification category. For example, his subgeneric classification is based mainly on structural variations (e.g., valve dehiscence type), and his species level classification on variations in size and shape.

In his revision Simpson did not explicitly state which species concept he was following, but, as the above discussion indicates, he was almost certainly using the morphological species concept. He appears to have adopted a particularly narrow species concept by recognising species and varieties on the basis of minor or trivial differences in pod and stem characters. Many of the species recognised in Simpson's revision, particularly in subgenus *Carmichaeliella,* are only of local or regional distribution and are part of the natural population variation associated with widespread and variable species. Unfortunately, Simpson's revision of *Carmichaelia* using a narrow morphological species concept has proven difficult to apply as there is more natural intra- and inter-population variation in the pods and branchlets than he was either aware of or prepared to accept.

The revision of *Carmichaelia* presented here uses the morphological species concept. However, in practice it is applied rather differently to that of Simpson because I give considerable emphasis to floral characters rather than those of the pods and cladodes (branchlets). The floral characters mostly include the length and width of the standard, keel, and wing petals, and their ratios. For particular species the floral characters are usually very uniform and have virtually no regional or geographic variation. The emphasis given to floral characters in species circumscriptions has allowed for the development of a classification that accommodates intra- and inter-population variation in pod and cladode characters. In comparison to Simpson, I have applied the morphological species concept in a broad manner.

The recognition of groups of taxa is a significant step in completing the taxonomic

revision of *Carmichaelia*. In assigning these groups of taxa to a particular rank and in developing a classification it is necessary to be consistent in giving similar characters the same emphasis. For example, I generally considered floral characters to be more important and reliable than fruit or vegetative characters. Therefore, species are recognised where groups are uniform and have consistent floral differences, where a distinct morphology is considered to reflect reproductive isolation, and where there is a well defined distribution and habitat. These principles generally worked for all species except *C. corrugata* and C. *uniflora*, and *C. australis* and *C. petriei*, two groups which have similar floral characters. The former two species differ in cladode size, shape, colour, and ecology, and the latter two in pod characters and seed persistence.

The morphological species concept as applied here to *Carmichaelia* is considered to provide a pragmatic, if somewhat conservative, solution to some historically difficult taxonomic problems. It should be possible to identify species from field collections without having to rely on knowing from which geographic area the specimen was collected. Therefore, although there may have been a loss of information due to less species of *Carmichaelia* being recognised, there is improved accuracy is the application of names.

The reduced number of species of *Carmichaelia* does not necessarily translate to a loss of information. Plant morphological variation and associated distribution patterns can be accommodated in species descriptions and appropriately illustrated. The illustrations may take the form of statistical and associated graphic representation or they maybe of the actual variation in particular characters. In some situations it may be appropriate to construct an infraspecific classification to represent natural variation. For example, it could be argued that for some species of *Carmichaelia* that variation in pods and cladodes could be accommodated by recognising subspecies or varieties.

In developing a classification it is important and necessary to recognise that there is often disparity between the continuity of evolution and natural population variation and the rigidly discrete levels of biological classification. For particularly variable groups is it necessary to thoroughly study them in order to ascertain the type of variation present: Is the variation continuous? Can discrete components be distinguished? Unless the group is thoroughly studied it could be easy to conclude that the ends of a continuous range of intergrading forms are so distinct they warrant formal taxonomic recognition. It is also important to be consistent and apply the particular criteria used

for infraspecific taxa equally across all species being studied.

I considered developing an infraspecific classification for several species of *Carmichaelia* (e.g., *C. australis*) using characters of the pod, particularly their shape and size. The main reason for not taking this action for *C. australis* is that a careful study of variation from throughout the range of the species confirmed the pods vary in a continuous manner, although they also have a strong geographic bias. There are about six main geographic variants that could have perhaps been named as subspecies. However, there would have still been a considerable number of plants that would have been "intermediate", and so there would have been too many exceptions (unclassifiable plants) for the classification to work. Furthermore, the geographic locality of the collection would still be an important diagnostic attribute. The taxonomy and classification of Simpson (1945) for subgenus *Carmichaeliella* reflects this geographic bias, and many of the species he recognised are now considered to be regional variants of the widespread *C. australis*. The variation in *C. australis* can probably be explained as being the result of locally differentiating races forming due to strong environmental gradients and self-compatibility. Nevertheless, there is continuous variation which results from gene flow between populations from the different geographic areas and the probable weakening of environmental gradients near their periphery.

Another example of a variable species is provided by *C. juncea* which I accept as being widespread and variable in terms of pod size and shape. However, Simpson recognised this as a complex of six species and one variety, each from a different region. I consider that he over-emphasised the importance of pod size and shape and branchlet width and length in his circumscriptions of the six species and one variety.

Distribution patterns can also provide information that can be used to assist in the determination of rank, and therefore they contribute to species concepts. For example, sympatric taxa are generally accepted at the rank of species. The argument being applied here is that two or more taxa can occur in the same geographic area and remain morphologically and genetically distinct due to ecological or reproductive isolation. Sympatry can itself be better understood by providing information on whether the species are allotopic or syntopic. Allotopy refers to species growing in different habitats, and syntopy to species growing in the same habitat. This distinction is useful for species that are considered to be sympatric, because species that are allotopic are most likely to be separated spatially and therefore will not often come into contact. On

the other hand syntopic species will usually be in close proximity to each other.

Allopatric taxa can be treated as either species or subspecies, with the application of rank depending on the type of characters that support the different taxa and the personal preferences of the taxonomist. For example, vegetative or growth habit differences between allopatric taxa may be treated at the rank of subspecies, and floral differences at species rank. With allopatry the basic argument is that the taxa maintain their differences by spatial separation, and as they do not come into contact they do not need reproductive or other ecological separation.

Extant distribution patterns reflect contemporary distributions and can clearly be used to assist in the application of rank, but they cannot be used to infer the evolutionary processes that lead to speciation. For example, species that are currently sympatric may have evolved in an allopatric setting due to geographic fragmentation or habitat separation. At some later time they became sympatric due to further geographic or habitat changes.

In the revision of *Carmichaelia* presented here allopatric and sympatric distribution patterns occur. Allopatry occurs among closely related species belonging to a number of Simpson's different subgenera. For example, *C. compacta*, *C. curta*, and *C. juncea* of subgenus *Huttonella* are allopatric, as are *C. astonii*, *C. monroi*, and *C. vexillata* of subgenus *Monroella*. Each of these species has a number of distinct floral and vegetative morphological attributes that support their recognition at species rank rather than subspecies. Species from the different subgenera are frequently sympatric and often syntopic. For example, at MacKenzie Pass, Canterbury, *C. corrugata* (*Suterella*), *C. nana*, (*Enysiella*), *C. monroi* (*Monroella*), and *C. australis* (*Carmichaelia*) occur together on the one site and in the same habitat.

In summary, by applying the morphological species concept to *Carmichaelia* in a broad manner, with particular emphasis on floral characters, and accepting natural variation in pods and cladodes, it is possible to recognise discontinuities in growth habit, vegetative, floral, and fruit characters. Species can be clearly defined and recognised by a combination of qualitative and/or quantitative characters, and they can also accommodate a considerable amount of natural variation.

3.5 *CARMICHAELIA* REVISION

Carmichaelia R.Br., in J. Lindley, *Bot. Reg. 11*, t. 912 (1825)

TYPE SPECIES: *Carmichaelia australis* R.Br., in J. Lindley, *Bot. Reg. 11*, t. 912 (1825)

Small trees, shrubs, or dwarf shrubs, sometimes rhizomatous or lianoid. Juveniles with or without habit-heteroblastic development; when present stems erect, spreading, or decumbent, and thin, flexuose, and leafy. Wood with vessels and axial parenchyma in storied structure, vessels with helical thickenings and simple perforation plates, axial parenchyma mainly fusiform and with gable ends, ray parenchyma heterocellular, and pith persistent and circular or compressed. Cladodes compressed or terete, sometimes grooved; stomata abundant, transverse. Adult plants usually leafless, the leaves being replaced by scales formed by the fusion of the stipules. Leaves unifoliolate, or compound and 1-9-foliolate; often heteroblastic; stipels absent; pulvinus absent. Inflorescences lateral, 1 or more per node, racemose, sometimes branched, flowers 1-many. Flowers zygomorphic, hermaphrodite. Calyx campanulate, hairy or glabrous, 5-lobed. Corolla papilionaceous. Stamens 10, diadelphous; anthers bilocular or unilocular, uniform. Style glabrous or bearded on the adaxial surface. Stigma capitate, sometimes fringed with hairs. Fruit with replum, suture not intruded, dorsiventrally or laterally compressed; valves indehiscent, partially-dehiscent, or fully dehiscent, few- to many-seeded. Seeds reniform, oblong, or elliptic. Chromosome numbers $2n = 32, 96$.

1. ***Carmichaelia appressa*** G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 263-64 (1945)

DESCRIPTION (Fig. 3.6): Prostrate, occasionally decumbent, densely branched shrub, 25(–40) cm × 1–1.5(–2) m. Branches 30–75(–100) cm long and up to 30 mm diameter, prostrate or weakly decumbent. Cladodes 50–100(–150) × 1–2 mm, prostrate, sometimes weakly ascending, linear, striate, compressed, weakly plano-convex, light green to green-yellow, sparsely hairy to glabrous, apex subacute or obtuse; leaf nodes 7–11. Leaves 1–3–foliolate, present on seedlings and rarely on adults, terminal leaflet larger; lamina 2-5 × 1-2.5 mm, obovate, fleshy, green, adaxial and abaxial surfaces

sparsely to moderately hairy, apex emarginate, base cuneate; petiole 1-11 mm long, sparsely hairy, green; petiolule < 0.25 mm long, glabrous, light green. Leaves on cladodes reduced to scales, < 0.5 mm long, broad-triangular, glabrous, apex subacute, margin hairy. Stipules c. 0.5 × c. 0.5 mm, free, triangular, adaxial surface glabrous, abaxial surface glabrous or with a few scattered hairs and becoming glabrous with age, apex acute, margin hairy. Inflorescence a raceme, 1–2(–3) per node, each with (2–)5–7(–13) flowers. Peduncle 1–8.5 mm long, glabrous or sparsely hairy, green, occasionally flushed red. Bracts < c. 0.5 mm long, triangular, glabrous, apex acute, margin hairy. Pedicel 2-4 mm long, glabrous to sparsely hairy, pale green. Bracteoles on upper part of pedicel, lanceolate, glabrous, green, occasionally flushed red, apex subacute, margin hairy. Calyx c. 1.5 × 1.8-2 mm, campanulate, green, outer surface glabrous to sparsely hairy. Calyx lobes 0.2–0.3 mm long, triangular, inner surface glabrous, appressed to corolla, apex acute. Bud green or white. Standard 4-5 × 5-6 mm,obovate, patent, positioned in central part of keel, keeled, apex retuse; inner surface with a purple blotch, white margins, purple-veined; outer surface white, green at base, purple-veined; claw c. 1 mm long, pale green. Wings 4-5 × 1.75-2 mm, oblong, longer than keel, apex obtuse; inner and outer surfaces white, and purple-veined; auricle rounded, white; claw c. 1.5 mm long, pale green. Keel 3.5–4 × c. 1.5 mm, apex obtuse; distal part of inner and outer surfaces purple, proximal part white; auricle < 0.5 mm long, rounded, pale green; claw c. 1.5 mm long, pale green. Stamens 3-3.75 mm long; dorsal filaments connate for ⅞ of length, outer stamens free for c. 0.5 mm. Pistil c. 4 mm long, exserted beyond the stamens, glabrous; ovules 5-8. Pods 8-12 × 3-4 mm, elliptic to broad-oblong, laterally compressed, spreading, brown or grey, valves dehiscent; beak c. 1 mm long, in a central apical position, stout, pungent-tipped. Seeds c. 2 × c. 1.5 mm, reniform, 2-5 per pod, dark purple or black, usually persistent on replum. Chromosome number $2n = 32$ (Dawson 1989). FL Oct–Jan, FT Dec–May.

DISTRIBUTION AND HABITATS (Fig. 3.6, 3.23): *Carmichaelia appressa* is restricted to Kaitorete Spit, Canterbury. It grows on gravelly sandy loam, stabilised sand dunes, and ridges of sand which represent the former shores of Lake Ellesmere. The plant most commonly occurs on immature soils without top soil development (sand flats) behind mobile foredunes where *Desmoschoenus spiralis* is the principal native plant. It does not occur on adjacent older soils with a developed top soil or among grey scrub

Fig. 3.6 *Carmichaelia appressa*, Kaitorete Spit, Canterbury.

communities where the dominant plants are *Coprosma propinqua*, *Discaria toumatou*, *Melicytus alpinus*, and *Muehlenbeckia complexa*.

RECOGNITION: *Carmichaelia appressa* is distinguished from *C. australis* on Kaitorete Spit by its prostrate growth habit and yellow-green cladodes. *Carmichaelia australis* has been observed growing on developed soils with a top soil up to 25 cm deep. Plants of *C. appressa* and *C. australis* can often be found within 10–40 metres of each other on their respective soil types. The rhizomatous *C. corrugata* is also on Kaitorete Spit, where it occurs with *C. appressa* on some sand and Taumutu gravel ridges.

Damage to *C. australis* by browsing, wind, and salt spray often results in a low-spreading and suckering bush which can be wrongly interpreted as an intermediate form between the shrubby *C. australis* and the prostrate *C. appressa*.

VARIATION: Some plants of *C. appressa* have a very flat appearance with their branches and cladodes appressed to the ground, whereas others have prostrate branches but the cladodes are decumbent or weakly ascending.

REPRESENTATIVE SPECIMENS: CANTERBURY: Lake Forsyth, *R. M. Laing*, Easter 1922, CHR 45849; Kaitorete Spit, *R. O. Gardner*, 4 Mar 1986, CHR 432156; Kaitorete Spit, *H. D. Wilson*, 30 Jan 1987, CHR 478772.

ETYMOLOGY: The epithet *appressa* refers to the branches and cladodes being close to and often flatly pressed against the ground.

ILLUSTRATION: Wilson & Galloway (1993, fig. 70g).

CONSERVATION STATUS: On Kaitorete Spit the habitat of *C. appressa* is very susceptible to damage by off-road motorbikes and 4WD vehicles and excavation for sand. However, as *C. appressa* is reasonably abundant the classification of local by Cameron et al. (1995) is supported.

DISCUSSION: Two groups of prostrate, sprawling, and low-growing plants which appear

to be closely related to *C. appressa* occur on the Canterbury plain and on the braided riverbeds responsible for the building of the plain. A decumbent, straggly, and sprawling *Carmichaelia* is restricted to recently deposited or disturbed alluvial river gravels in the upper Rangitata River catchment. Another prostrate and sprawling form occurs on the upper part of terrace risers of streams leading to the high coastal cliffs between the Rakaia and Rangitata rivers. In contrast to *C. appressa* this plant frequently scrambles among *Coprosma propinqua, Discaria toumatou*, and *Melicytus alpinus*. In the immediate vicinity of each of these distinctive plants is *C. australis*. The relationship between these two entities, *C. appressa* and *C. australis*, is being further investigated. Preliminary evidence suggests that the mountain-building phase of the Southern Alps, the glaciation and eroding of the mountains, and the building of the Canterbury plain have created new habitats which have been available for colonisation and have stimulated speciation. On different soil types and surfaces of different age selection appears to have independently favoured a low-growing and prostrate growth habit. However, floral and fruit differentiation has not occurred, the flowers and fruit of the two unnamed forms and *C. appressa* being indistinguishable from Canterbury populations of *C. australis*.

A high degree of ecological specialisation or association with unique geological features is not uncommon among the New Zealand broom species. *Carmichaelia astonii* (Heenan 1995a), *C. hollowayi* (see below), and *Notospartium glabrescens* (Heenan unpubl. data) prefer to grow on base-rich substrates, and the closely related and allopatric *C. corrugata* and *C. uniflora* occur on specific soil types (Heenan 1995a).

2. *Carmichaelia arborea* (G.Forst.) Druce, *Bot. Soc. Exch. Club Brit. Isles 4 Supplement 1916*, 612 (1917)

≡ *Lotus arboreus* G.Forst., *Fl. ins. austr.*, 52 (1786).

= *C. australis* var. τ *grandiflora* Hook.f., *Fl. nov.-zel.* 1, 50 (1852) ≡ *C. grandiflora* (Hook.f.) Hook.f., *Handb. N. Zeal. fl.*, 49 (1864).

= *C. grandiflora* var. *alba* Kirk, *Stud. fl. New Zealand*, 111 (1899).

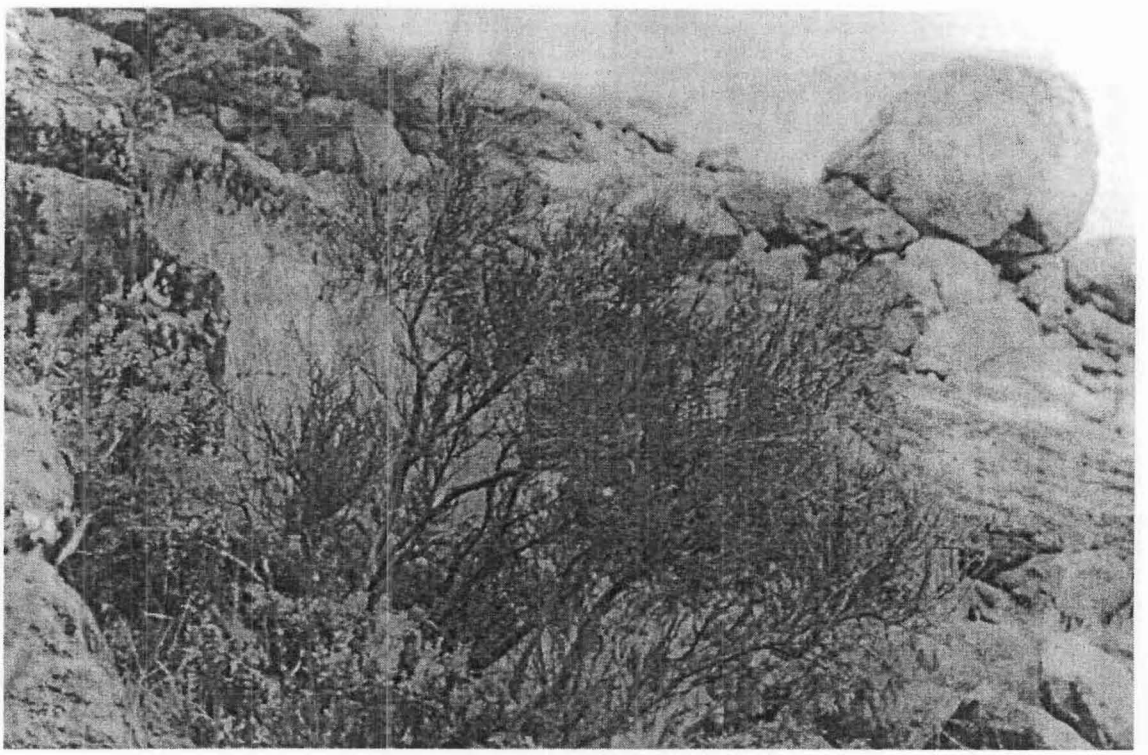


Fig. 3.7 *Carmichaelia arborea*, Mt Cook, Canterbury.

= *C. grandiflora* var. *dumosa* Kirk, *Stud. fl. New Zealand*, 111 (1899).

DESCRIPTION (Fig. 3.5, 3.7): Shrub, up to 2 m × 2 m; sometimes suckering and forming broad patches up to 1 m tall. Branches up to 80 mm diameter, stout, ascending and spreading. Cladodes 70–150 × 1.5–3 mm, erect to spreading, sometimes drooping, rarely divaricate, linear, striate, compressed, green to dark green, sometimes hairy when young, glabrous when mature, apex obtuse; leaf nodes 4–11. Leaves 1–3(–5)–foliolate, present on seedlings and on adult plants, terminal leaflet larger; lamina 2–7 × 1–4.5 mm, obovate, broad-obovate to broad-elliptic, fleshy, green, adaxial surface glabrous, abaxial surface glabrous or with a few scattered hairs, apex emarginate, base cuneate; petiole 7–11 mm long, glabrous except for a tuft of hairs at petiolule base, green; petiolule < 0.5 mm long, glabrous, light green. Leaves on cladodes reduced to scales, < 0.8 mm long, broad-triangular, glabrous, apex subacute. Stipules 0.9–1.3 × 1–1.4 mm, free, triangular, glabrous, apex subacute with a tuft of hairs, margin hairy. Inflorescence a raceme, 1 per node, each with 5–9(–10) flowers clustered on upper third of raceme. Peduncle c. 8 mm long, glabrous, green. Bracts < 1 mm long, triangular, pale brown,

adaxial surface hairy, abaxial surface glabrous, apex acute to subacute, margin hairy. Pedicel 1–1.5 mm long, glabrous, green. Bracteoles < 0.5 mm long, on upper part of pedicel or on receptacle, pale brown, adaxial surface hairy, abaxial surface glabrous, apex subacute to obtuse and with tuft of hairs. Calyx 3–3.5 × 2–2.5 mm, campanulate, green, outer surface glabrous. Calyx lobes 0.5–1 mm long, triangular, inner surface hairy, appressed to corolla, apex acute. Standard 6–6.5 × 7–8 mm, broad-obovate,patent, positioned towards front of keel, keeled, apex retuse or obtuse with an apiculate tip; white or with a pale central blotch, veins sometimes weakly flushed red-purple; claw c. 1 mm long, pale green. Wings 6–7 × 1.5–2 mm, oblong, longer than keel, white, apex obtuse; auricle 0.2–0.3 mm long, triangular; claw 1.8–2 mm long, pale green. Keel 5–6 × 1.5–1.8 mm, white, apex obtuse; auricle 0.3–0.5 mm long, triangular,white; claw 2–2.5 mm long, pale green. Stamens 4.5–5 mm long; dorsal filaments connate for c. ¾ of length, outer stamens free for c. 0.8 mm. Pistil 5–6 mm long, exserted beyond stamens, glabrous; ovules 8–9(–11); stigma with a ring of hairs at base. Pods 7–15 × 2.7–4.5 mm, oblong or broad-oblong, laterally compressed, erect, light grey or pale brown, both valves dehiscent at distal end; beak 2–2.5 mm long, in a central apical position, stout, pungent-tipped. Seeds 2–3.7 × 1.6–2.4 mm, broad-oblong to broad-elliptic, 1–3 per pod, surface with 1–3 ridges, testa thin and membranous, light brown or tan. Chromosome number $2n = 32$ (Dawson 1995). FL Dec–Mar, FT Jan–Dec.

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia arborea* is most common along and west of the Main Divide in Westland, Canterbury, Otago, and Southland; it is rare to the east of the Main Divide in Canterbury. It occurs in a variety of habitats including glacial moraine and outwash, river terraces, subalpine scrub, rock outcrops and cliffs, forest margins, and disturbed surfaces such as are created by landslips and erosion.

RECOGNITION (Fig. 3.6): *Carmichaelia arborea* and *C. odorata* are recognised by their erect flowering and fruiting peduncle and rachis, erect pods which are dehiscent in the distal part and flattened seeds which lack a thick testa. *Carmichaelia arborea* is distinguished from *C. odorata* in having a shorter peduncle and rachis, fewer flowers, a larger flower with the keel 5–6 mm long (in *C. odorata* 3.5–4 mm long), a white flower which sometimes has a pale mark on the central part of the standard, and larger pods.

VARIATION: The size of the pods varies throughout the range of the species; they are up to 15 mm long in southern areas (e.g., CHR 198203), but usually 7–9 mm long in plants from more northern areas (e.g., CHR 309220). The plants are usually spreading or upright shrubs with several main stems. However, plants of a low stature and with a strongly rhizomatous or suckering growth habit are sometimes seen.

REPRESENTATIVE SPECIMENS: CANTERBURY: Pudding Hill, *A. D. Lowe*, 15 Dec 1976, CHR 309220; West Mathias River, *B. Molloy*, 23 Jan 1979, CHR 386654; Hooker River, *D. Petrie*, Mar 1911, CHR 11823; Sealy Range, *A. M. Buchanan*, Dec 1968?, CHR 252892; WESTLAND: Waiho River, *K. F. O'Connor*, 22 Sep 1971, CHR 223615a; OTAGO: Siberia River, *P. J. Harrigan*, 5 Jan 1953, CHR 78837; SOUTHLAND: Milford Sound, *R. M. Laing*, CHR 4144; Wilmot Pass, *M. J. A. Simpson 1420*, 20 Feb 1959, CHR 111945.

ETYMOLOGY: The epithet *arborea* was given by Forster because he regarded this plant as a woody or arborescent species of *Lotus*, a genus of herbs and subshrubs.

ILLUSTRATIONS: Eagle (1982, fig. 78) and Wilson & Galloway (1993, fig. 71a), as *C. grandiflora*.

CONSERVATION STATUS: Not threatened.

3. *Carmichaelia astonii* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 276-277 (1945)

DESCRIPTION (Fig. 3.4, 3.8): Dwarf and spreading shrub, up to 0.2 × 0.5 m. Branches stout, ascending and horizontal, 10-25 mm diameter. Cladodes linear, striate, compressed, erect to spreading, green to green-bronze, frequently hairy when young (hairs sometimes retrorse), 30-95 × 4-8 mm; apex subacute to obtuse, yellow to yellow-green; leaf nodes 2-4. Leaves simple, obovate to oblanceolate, fleshy, green or green-bronze, present on seedlings, but absent on adult plants, 6-8 × 2-5.5 mm; adaxial and abaxial surfaces hairy; apex emarginate to retuse; base cuneate; petiole hairy, c. 2 mm

long. Leaves on cladodes reduced to a scale, triangular, glabrous, < 0.5 mm long; apex acute. Stipules free, triangular, 0.9-1 × 0.7-0.8 mm; adaxial surface glabrous; abaxial surface hairy, becoming glabrous with age; apex acute; margin hairy. Inflorescence a raceme, 1-2(-4) per node, each with (1-)2-3(-4) flowers. Peduncle hairy, green, 7-8 mm long. Bracts triangular, glabrous, pale green, < 1 mm long; apex acute; margin hairy. Pedicel hairy, pale green, 2.5-8 mm long. Bracteoles at top of pedicel, green and occasionally flushed red, < 0.5 mm long; apex acute; margin hairy. Calyx campanulate, 4.5-5.5 × c. 2 mm; inner surface glabrous, green; outer surface hairy, green and occasionally flushed red. Calyx lobes narrow-triangular, green and usually flushed red, 2-2.5 mm long; adaxial surface densely hairy; apex acute; two upper lobes usually appressed to base of standard; three lower lobes spreading away from keel. Standard obovate, patent, positioned in central area of keel, weakly keeled, margins recurved, c. 12 × c. 8 mm; central area of adaxial surface purple, margins white, sometimes purple-veined; abaxial surface white with a darkened central part; claw pale green, c. 3 mm long; apex emarginate and occasionally mucronulate. Wings oblong, shorter than keel, c. 9 × c. 2.5 mm; distal area of adaxial surface purple, proximal area pale green; abaxial surface white, purple-veined; auricle triangular, pale green, 1-1.25 mm long; claw pale green, 2.5-3 mm long; apex acute. Keel c. 10 × c. 3.5 mm; distal area of adaxial surface purple, proximal area white or pale green; auricle triangular, pale green, c. 1 mm long; apex obtuse; claw pale green, 3.5-4 mm long. Stamens 9-11.5 mm long; lower filaments connate for c. ⅔ length and with outside filaments free for 4-4.5 mm. Pistil exserted beyond stamens, c. 12 mm long; style bearded on upper surface; ovary weakly falcate, glabrous; ovules (8-)13-14(-16). Pod oblong or oblanceolate, laterally compressed, light grey or brown, one or both valves often partially dehiscent at proximal end, 14-21(-23) × 4-6(-7.5) mm; beak on adaxial suture, stout, pungent, 1-2 mm long. Seeds oblong-reniform, (4-)6-8 per pod, olive green, green-yellow, or dull yellow, occasionally mottled black, 2.5-3.5 × 1.5-3 mm. Chromosome number $2n = 32$ (Dawson 1989). FL Jan-Dec, FT Dec-Apr.

DISTRIBUTION AND HABITAT (Fig. 3.8, 3.24): Marlborough. Restricted to rendzina and related steepland soils of medium to high fertility and derived from Amuri Limestone. Described as a "strong calcicole" by Druce & Williams (1989).

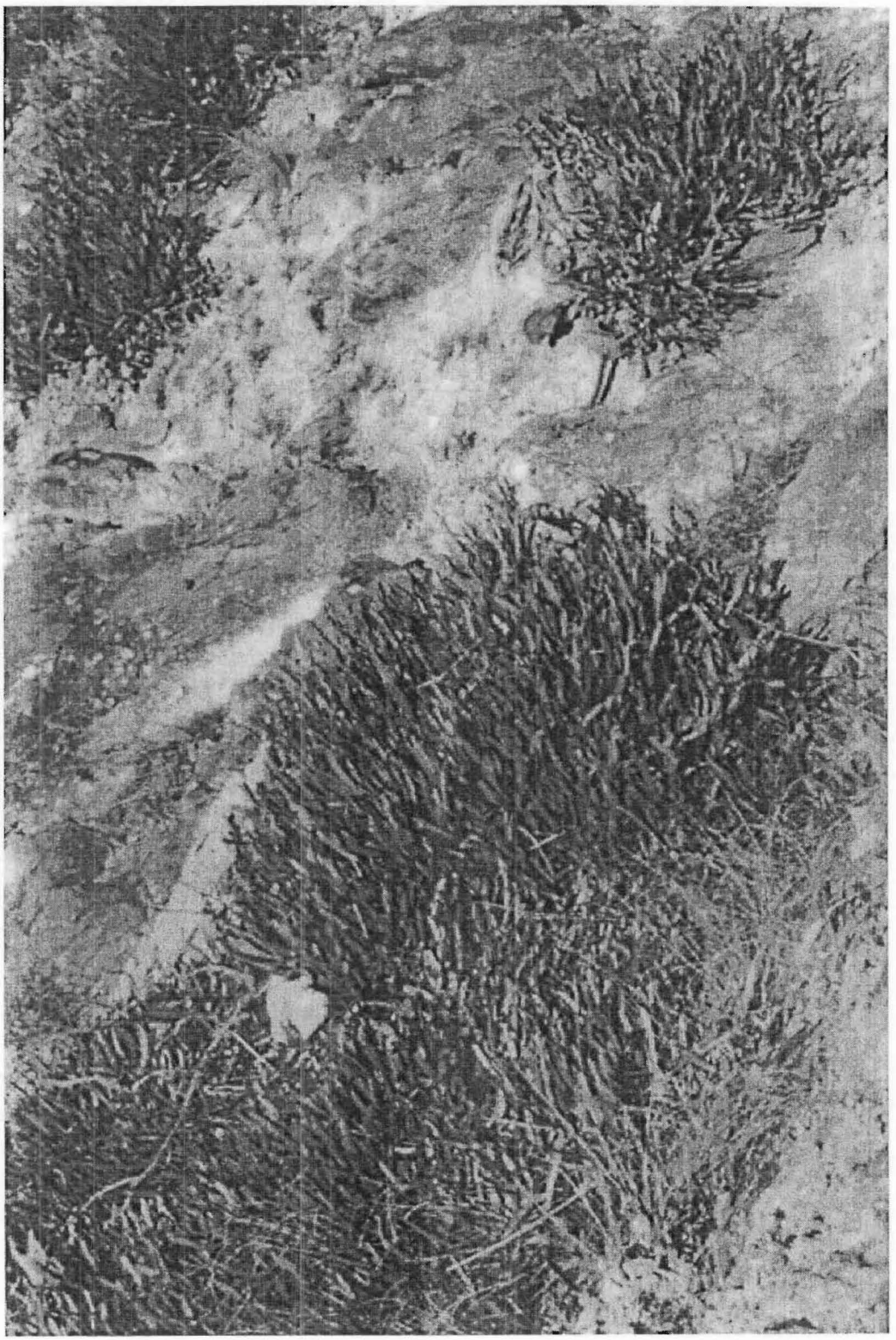


Fig. 3.8 *Carmichaelia astonii*, Ward, Marlborough.

RECOGNITION (Fig. 3.4): *C. astonii* is a dwarf shrub distinguished from the similar *C. monroi* and *C. vexillata* by its more robust habit; stouter cladodes; larger calyx, petals and pods; and by the long lower calyx lobes which spread away from the keel.

VARIATION: Cladode size and colour varies in the Ward population, and throughout the range of the species.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Mead Gorge *L. Cockayne ex B. C. Aston*, Dec 1915, CHR 18379; Clarence Valley, *B. C. Aston*, Dec 1915, CHR 331948; Mead Hill, SW of Chalk Ra., *A. P. Druce*, Jan 1976, CHR 279271; mouth of Flaxbourne R., *A. P. Druce*, Apr 1975, CHR 277521; Mt Benmore, *A. P. Druce*, Nov 1973, CHR 249180.

ETYMOLOGY: The specific epithet *astonii* commemorates B. C. Aston (1871-1951), who first collected the plant from the Mead Gorge, Marlborough.

CONSERVATION STATUS: Although restricted to a small geographical area in eastern Marlborough and to soils derived from Amuri limestone, this species comprises several moderate-sized populations. Browse damage from goats, possums, and sheep is frequently observed (S. Courtney, pers. comm. May 1994). Listed by Cameron et al. (1993) as a local plant, and not regarded as threatened.

4. *Carmichaelia australis* R.Br., in J. Lindley, *Bot. Reg. 11*, t. 912 (1825)

= *C. acuminata* Kirk, *Stud. fl. New Zealand*, 114 (1899) ≡ *C. flagelliformis* var. *acuminata* (Kirk) Cheeseman, *Man. New Zealand fl.*, 117 (1906).

= *C. aligera* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 250-251 (1945).

= *C. arenaria* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 252-253

(1945).

= *C. australis* var. *alata* Kirk, *Stud. fl. New Zealand*, 110 (1899).

= *C. australis* var. *egmontiana* Cockayne et Allan, *Trans. & Proc. New Zealand Inst. 56*, 21 (1926) ≡ *C. egmontiana* (Cockayne et Allan) G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 255 (1945).

= *C. australis* var. *strictissima* Kirk, *Stud. fl. New Zealand*, 110 (1899).

= *C. corymbosa* Colenso, *Trans. & Proc. New Zealand Inst. 21*, 80 (1889) ≡ *C. flagelliformis* var. *corymbosa* (Colenso) Kirk, *Stud. fl. New Zealand*, 114 (1899).

= *C. cunninghamii* Raoul, *Choix. pl. Nouv.-Zél.*, 29, t. 28B (1846).

= *C. flagelliformis* Benth., in J. D. Hooker, *Fl. nov.-zel. 1*, 51 (1852).

= *C. hookeri* Kirk, *Stud. fl. New Zealand*, 114 (1899) ≡ *C. flagelliformis* var. *hookeri* (Kirk) Cheeseman, *Man. New Zealand fl.*, 117 (1906).

= *C. micrantha* Colenso, *Trans. & Proc. New Zealand Inst. 26*, 313 (1894).

= *C. multicaule* Colenso, *Trans. & Proc. New Zealand Inst. 25*, 329 (1893).

= *C. ovata* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 260 (1945).

= *C. paludosa* Cockayne, *Trans. & Proc. New Zealand Inst. 47*, 113 (1915).

= *C. rivulata* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 264-265 (1945).

= *C. robusta* Kirk, *Stud. fl. New Zealand*, 114 (1899).

= *C. silvatica* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 251 (1945).

= *C. solandri* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 253-254 (1945).

= *C. stricta* C.B.Lehm., *Hamburger Garten- Blumenzeitung 8*, 372 (1852).

= *C. subulata* Kirk, *Stud. fl. New Zealand*, 112-113 (1899).

= *C. violacea* Kirk, *Stud. fl. New Zealand*, 112 (1899).

DESCRIPTION (Fig. 3.1, 3.2, 3.3, 3.5, 3.9, 3.10): Shrub, 2–3(–8) × 2–3(–5) m. Branches up to 100 mm diameter, ascending and spreading. Cladodes 30–200 × 1.5–8 mm, ascending or spreading, linear, striate, weakly plano-convex to strongly flattened and compressed, green, yellow-green, or brown-green, glabrous to sparsely hairy, apex obtuse to subacute; leaf nodes 4–15. Leaves 1–3–foliolate, present on seedlings and rarely on adults, terminal leaflet larger; lamina 3–12(–22) × 1.3–7(–16) mm, obovate to oblong, fleshy, green, sometimes with dark mottling, adaxial and abaxial surfaces glabrous to moderately hairy, apex emarginate, base cuneate; petiole 1–10 mm long, glabrous to moderately hairy, green; petiolule < 0.25 mm long, glabrous or sparsely hairy, light green. Leaves on cladodes reduced to scales, < 0.5 mm long, broad-triangular, glabrous, apex subacute, margin hairy. Stipules c. 1 × c. 1.5 mm, free, broad-triangular, adaxial surface glabrous, abaxial surface glabrous or with few scattered hairs and becoming glabrous with age, apex subacute, margin hairy. Inflorescence a raceme, 1–3 per node, each with 4–15 flowers. Peduncle 1–10 mm long, glabrous to moderately hairy, green, occasionally flushed red. Bracts < c. 0.5 mm long, triangular, glabrous, apex acute, margin hairy. Pedicel 2-4 mm long, glabrous to sparsely hairy, pale green. Bracteoles on upper part of pedicel or lower part of receptacle, lanceolate, glabrous, green and often flushed red, apex subacute, margin hairy. Calyx 1.3–1.7 × 1.7-2.2 mm, campanulate, green, outer surface glabrous to moderately hairy. Calyx lobes 0.2–0.4 mm long, triangular, inner surface glabrous, appressed to corolla or rarely weakly spreading, apex acute. Standard 4-6 × 5-6.5 mm, obovate, patent, positioned in central part of keel, keeled, apex retuse; inner surface white, sometimes with a purple blotch,

purple-veined; outer surface white, green at base, purple-veined; claw c. 1 mm long, pale green. Wings 4-5 × 1.7-2.2 mm, oblong, longer than keel, apex obtuse; inner and outer surfaces white, purple-veined; auricle rounded, white; claw c. 1.5 mm long, pale green. Keel 3.2–4.2 × c. 1.5 mm, apex obtuse; distal part of inner and outer surfaces purple, proximal part white; auricle < 0.5 mm long, rounded, pale green; claw c. 1.5 mm long, pale green. Stamens 3-4 mm long; dorsal filaments connate for c. three-quarters of length, outer stamens free for c. 0.5 mm. Pistil c. 4 mm long, exserted beyond the stamens, glabrous; ovules 5-10. Pods 6.5–15 × 2–5.5 mm, oblong, broad-oblong, elliptic, broad-elliptic, or sometimes orbicular, laterally compressed, erect or spreading, brown, grey, or black, valves dehiscent; beak 0.5–2.5 mm long, in a central apical position, stout, pungent-tipped. Seeds 2.2–4 × 1.7–2.8 mm, oblong to reniform, 1–5 per pod, orange, red, green, or yellow-green and often with black mottling, usually persistent on replum. Chromosome number unknown. FL Oct–Feb, FT Nov–May.

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia australis* is widespread throughout mainland New Zealand except the southern part of the South Island. It occurs on coastal, lowland, and montane river terraces, stream banks, colluvium slopes, among tussock grassland and grey scrub, on the edge and margins of dense bush, forest, and swamps, and among rock outcrops.

RECOGNITION (Fig. 3.6): *Carmichaelia australis* is an upright or spreading shrub with erect, spreading or drooping pods, the pod valves usually dehiscent when mature and the seeds remaining attached to the replum.

There are six other shrubby species of *Carmichaelia* with which *C. australis* could be confused. *Carmichaelia williamsii* is restricted to the Bay of Plenty coast and islands in the Hauraki Gulf, and has broad, flat stems and large yellow flowers; *C. petriei* occurs in Otago and Southland and has pendulous pods with the valves usually persistent, and seeds which detach readily from the replum; *C. odorata* and *C. arborea* occur in the lower North Island and northern and central South Island, and are recognised by their erect peduncle, rachis, and pods, the pods dehiscing only in the top part, and flattened seeds with a thin testa; *C. compacta* and *C. curta* have dorsiventrally compressed, indehiscent pods.

VARIATION: *Carmichaelia australis* exhibits a range of variation in several characters. This variation has a genetic basis, as cultivated plants will usually retain the particular features observed in the wild. The underlying reasons for this variation have not been studied, but they appear to have a geographical and/or environmental basis. Plants belonging to a particular population or geographic area and which exhibit one particular part of the species variation are usually linked by intermediate forms to plants in adjacent populations or geographic areas. Variation has been observed in the cladodes, growth habit, seeds, and pods.

Cladodes: Plants from the northern and western half of the North Island have flattened cladodes up to 8 mm wide, whereas plants from the central, eastern, and southern parts of the North Island and the South Island have terete or plano-convex cladodes 1.5–4 mm wide. In the North Island the gradation between the flattened and terete or plano–convex cladodes occurs in both north-south and west-east directions. In the South Island there is variation in cladode diameter; stout and pungent-tipped plants occurring in the Mackenzie Basin and upper parts of the Waitaki River valley, and slender and obtuse-tipped forms outside of these areas. Cladode colour also varies, for example in the South Island, where plants from eastern regions generally have yellow-green or brown-green cladodes and those from western parts have green.

Growth habit: Plants usually form erect and/or spreading shrubs. However, at Punakaiki and on the adjacent Seal Island in Westland plants have a spreading or decumbent growth habit and have been described by Simpson (1945) as *C. arenaria*. In cultivation these plants form small shrubs with an erect and spreading habit, a feature also noted by Simpson (1945). The growth habit of the wild plants is interpreted as a habitat-induced form which lacks a genetic basis.

Seed colour: The testa can be yellow-green, yellow-green or green with black mottling, or sometimes almost black in plants from the South Island and central, eastern, and southern North Island. The dominant colours in western and northern parts of the North Island are red or red-orange, often with black mottling. Some plants in northern Westland and NW Nelson also have red-orange seeds.

Radicle: Bending of the radicle and an associated twisting of the petiole within the seed

is a variable character which is best observed on germinating seeds. In populations in eastern parts of the North and South islands the radicle has either a single bend or no bend and the twist of the petiole is generally only weakly evident or absent. Some populations from the East Cape and Gisborne areas have plants with either a single fold or no fold of the radicle. In western populations of the North and South islands the twist of the petiole and bend of the radicle is more pronounced, and has been described by Simpson (1945) as a double fold. In some areas, such as parts of the central North Island, plants with a double, single, or no fold occur at the same locality. In the South Island variation in folding of the radicle is more pronounced because of the barrier of the Southern Alps; plants from the west coast have an obvious double fold, while those in central and eastern regions have a single or no fold.

Among the other species of broom in New Zealand *C. kirkii* consistently has a double fold of the radicle, as does *C. exsul* in the limited number of seeds available for examination. *Chordospartium*, *Corallospartium*, and *Notospartium* all exhibit a double fold of the radicle.

Pods: The pods feature a variety of sizes and shapes (Fig. 3.1, 3.2, 3.9, 3.10) which includes inter- and intra-population variation and more general patterns of regional variation linked by intermediate forms. Plants from Canterbury generally have long and narrow pods with a flattened upper replum; plants from Marlborough and the eastern North Island usually have shorter and ovate pods with a curved upper replum; plants from the west coast of the South and North islands are larger, stouter, and vary from rounded or orbicular in the North Island to elliptic or broad-elliptic in the South Island. Pod orientation is usually spreading, erect, or rarely drooping. Pods from the west coast of the North and South islands are predominantly erect, and seldom spreading or drooping. Beak length is also variable, with plants on the West Coast of the South Island having a longer beak (2–2.5 mm) than is typical (0.5–1.5 mm) for the species. A population near Mt Cavendish, Port Hills, Canterbury (NZMS260 M36/876358), provides an indication of intra-population variation. On 9 Mar 1995 examination was made of c. 100 plants along a transect of 150 metres. The pods vary considerably in size and shape (Fig. 3.10). The cladodes of the current season's growth also varied and were terete to plano-convex and 1.5–3 mm in diameter. Variation in pod shape and size has also been noted in the South

Island below Broderick Pass, Landsborough River (CHR 218506, 218509) and in the Manawatu Gorge, North Island (CHR 65171–65179).

REPRESENTATIVE SPECIMENS: NORTH AUCKLAND: Whangateau Harbour, *R. O. Gardener 4800*, 3 Feb 1986, CHR 432173; Whangarei, Aug 1878, *T. F. Cheeseman*, AK 4846; Waitakere Ranges, *L. M. Cranwell*, CHR 107907; Waitakere Ranges, May 1883, *T. F. Cheeseman*, AK 209795; Anawhata, *L. B. Moore*, AK 103140; SOUTH AUCKLAND: Kaimai Range, *A. P. Druce*, Apr 1982, CHR 389363; Lake Taupo, *G. I. Collett 30/70*, 19 Jul 1970, CHR 229625; TARANAKI: Mt Egmont, *A. P. Druce*, Sep 1963, CHR 159657; GISBORNE: Raukokore River, *S. Courtney*, 16 Jan 1985, CHR 418032; HAWKES BAY: Dannevirke, *A. P. Druce*, Aug 1966, CHR 165228; WELLINGTON: Tararua Range, *A. P. Druce*, Mar 1987, CHR 324000; Wainuiomata Valley, *A. P. Druce*, Sep 1966, CHR 165218; Titahi Bay, *G. Simpson*, 21 May 1939, CHR 41127c; MARLBOROUGH: French Pass, *B. H. Macmillan 68/184*, 17 Feb 1968, CHR 186567; CANTERBURY: Waipara, *A. J. Healy*, 16 May 1943, CHR 35254; Bankside Reserve, *B. P. J. Molloy*, 6 Jan 1970, CHR 201477; Dobson River, *G. Simpson*, AK 70624; WESTLAND: Wanganui Forest, *R. Melville*, 9 Apr 1962, CHR 144665; Jackson River, *E. H. Woods 87/44 & B. H. Macmillan*, 26 Jan 1987, CHR 455322.

ETYMOLOGY: The epithet *australis*, `southern', refers to the Southern Hemisphere.

ILLUSTRATIONS: *Carmichaelia australis* has been illustrated by Raoul (1846, as *C. australis* and *C. cunninghamii*), Eagle (1982, fig. 80 as *C. arborea*, fig. 81 as *C. flagelliformis*, fig. 83 as *C. robusta*, fig. 84 as *C. ramosa*, and fig. 86 as *C. aligera*), and Wilson & Galloway (1993, fig. 70b as *C. ovata*, fig. 70c as *C. rivulata*, fig. 70d as *C. robusta*, fig. 70e as *C. violacea*, and fig. 70f as *C. arborea*).

CONSERVATION STATUS: Not threatened.

DISCUSSION: The taxonomic history of *C. australis* is complex, as is indicated by the 25 synonyms. The main reasons for this are that new species have been described from single or few collections, and that little emphasis has been given to understanding

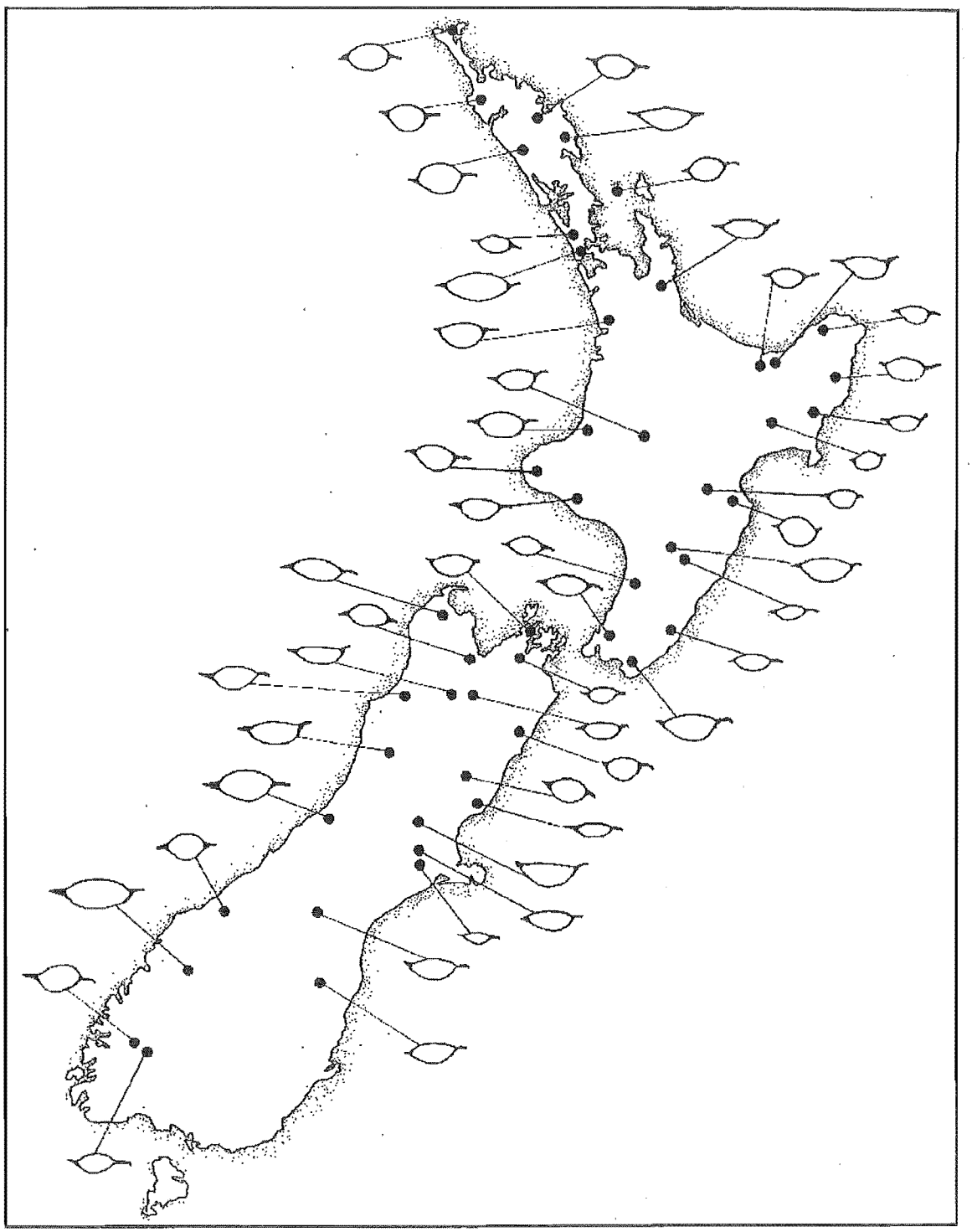


Fig. 3.9 Variation in pod shape and size of *Carmichaelia australis* from throughout New Zealand.

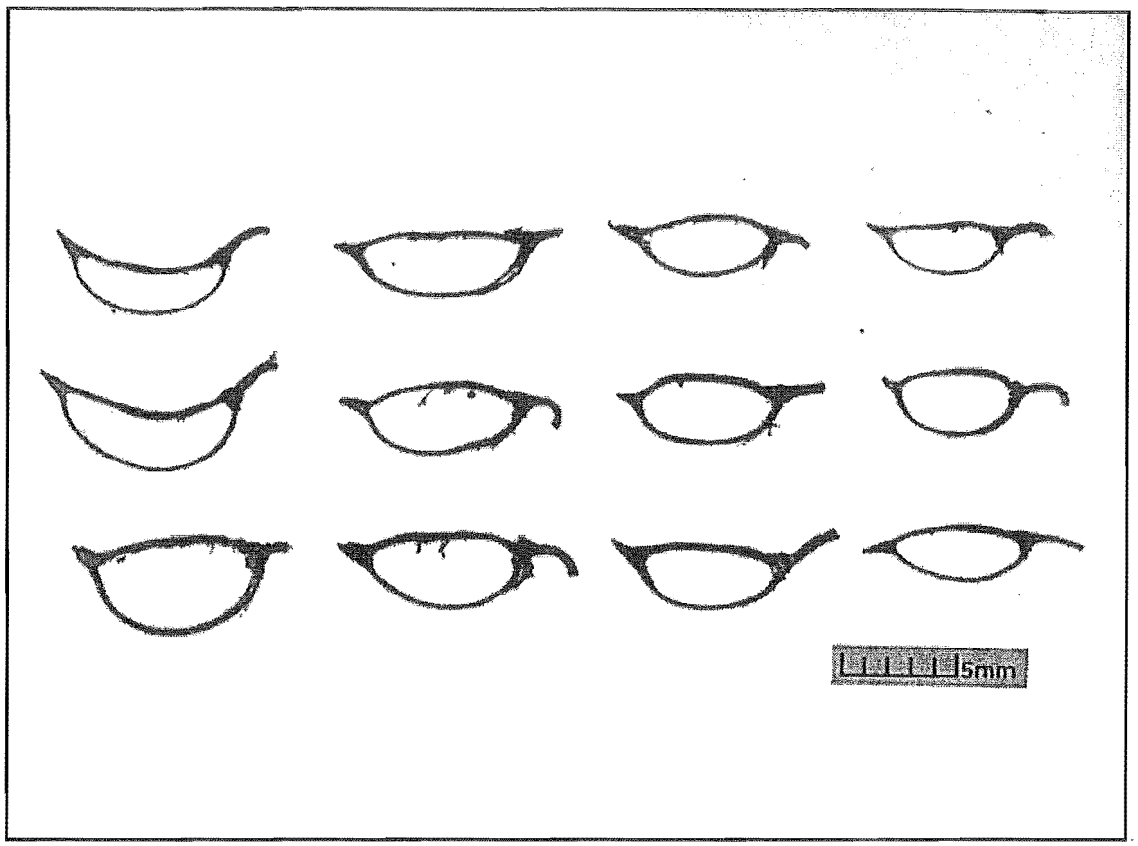


Fig. 3.10 Variation of pod shape and size in a single population of *Carmichaelia australis* collected from the Port Hills, Canterbury.

intraspecific and clinal variation. Regional variants have been recognised at species rank, with little regard to intermediate forms and variation within and between regions.

Consideration was given to applying a level of taxonomic rank to some of the variation within the *C. australis* complex. However, all characters show continuous variation in at least part of the geographical range of the complex. For example, on the west coast of the South Island the pods are usually erect, large, and with a prominent and centrally placed beak. These plants are distinct from Canterbury plants to the east of the Main Divide, which have pods that are usually spreading, smaller, and with a shorter beak that is offset from the centre. However, in Nelson the large pods of the west coast plants intergrade with those from Canterbury and the rounded and shorter pod typical of Marlborough plants.

Carmichaelia australis is regarded as an actively evolving complex of geographical and habitat-induced forms which are in the process of diverging into discrete taxonomic units. This process is more advanced in plants growing under extreme environmental and habitat conditions than in those with a geographical basis for their variation. For example, on Kaitorete Spit *C. appressa* is regarded as having diverged from *C. australis* to occupy a very specific and demanding habitat. In contrast, plants of *C. australis* from the East Coast of the North Island and Canterbury differ in pod shape and size, but these features are linked by a series of intermediate forms in Marlborough and Wellington.

In a study of flavonoids in *Carmichaelia*, Purdie (1984) concluded that the correlation between flavonoid chemistry and species boundaries was sometimes inconsistent, and that the distribution of flavonoids is predominantly geographical. Among the large shrubby species treated here as *C. australis*, Purdie (1984) identified two main groups, one eastern and one western, which differ in respect to the absence or presence of flavone C-glycosides. Using the names given by Purdie, in the eastern parts of New Zealand are *C. solandri*, *C. flagelliformis* (in part), *C. arborea* (in part), *C. ovata*, *C. robusta*, *C. violacea*, *C. rivulata*, and *C. ramosa*, and to the west are *C. aligera*, *C. silvatica*, *C. egmontiana*, *C. flagelliformis* (in part), and *C. arborea* (in part). This pattern of flavone C-glycoside distribution within *C. australis* appears to correlate with patterns of variation in morphological characters such as cladode diameter, seed colour, and degree of folding of the radicle.

Unfortunately, Purdie's work is of limited value as he did not deposit herbarium voucher specimens, and so the identification of the plant material analysed is somewhat tenuous. Furthermore, since the flavonoids in this study were incompletely identified there remains considerable doubt about taxonomic conclusions based on such data (Ken Markham pers. comm. May 1995). These factors may account for some unexpected differences in the results reported by Purdie, such as two flavone C-glycoside groups within *C. petriei* and three within *C. arborea* (sensu Purdie).

Morphological variation of the sort described for *C. australis* is not uncommon in the New Zealand flora; other examples are *Epilobium glabellum* (Raven & Raven 1976), *Haloragis erecta* (Forde 1964), *Ranunculus insignis* (Fisher 1965), *Sophora microphylla* (Godley & Smith 1977), and *Pittosporum obcordatum* (Clarkson & Clarkson 1994).

5. ***Carmichaelia compacta*** Petrie, *Trans. & Proc. New Zealand Inst. 17*, 272-273 (1885)

≡ *Huttonella compacta* (Petrie) Kirk, *Stud. fl. New Zealand,* 115 (1899).

= *C. compacta* var. *procumbens* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75,* 281 (1945).

DESCRIPTION (Fig. 3.4, 3.11): Erect or spreading shrub, up to 1-2 × 1-2 m, with densely placed branches and cladodes. Branches erect and spreading from base, 10-40(-60) mm diameter. Cladodes linear, striate, compressed, erect to spreading, green, glabrous, often crowded at ends of branches, 60-220 × 1.5-2.5 mm; apex subacute, yellow; leaf nodes 4-9. Leaves 1-9-foliolate, fleshy, obovate or sometimes ovate, hairy; adaxial surface mottled; abaxial surface green; apex emarginate to retuse; margin hairy; leaflets sessile or with short petiolule, 1.5-7 × 1-6.5 mm; petiole hairy, 8-16 mm long. Leaves on cladodes reduced to a scale, triangular, glabrous, < 0.5 mm long; apex acute. Stipules clasping shoot, triangular, 0.4-0.5 × 0.4-0.5 mm; adaxial surface glabrous; abaxial surface hairy, becoming glabrous with age; apex subacute to obtuse; margin hairy. Inflorescence a raceme, 1 per node, each with (3-)5-6 flowers. Peduncle glabrous to sparsely hairy, green, 7-16 mm long. Bracts triangular to narrow-triangular, pale green becoming membranous, 0.5-1 mm long; apex acute to subacute; margin hairy. Pedicel glabrous, pale green, 2-4 mm long. Bracteoles at base of receptacle or on upper part of pedicel, narrow-triangular, green and flushed red, glabrous, 0.4-0.8 × 0.1-0.3 mm; apex acute; margin hairy. Calyx campanulate, c. 1.5 × c. 1 mm; inner and outer surfaces glabrous, green, usually flushed with red. Calyx lobes triangular, flushed red, c. 0.5 mm long; apex acute; margin hairy. Bud white to pale purple. Standard obovate, spreading above wings and keel, 3-4 × 3.5-4.5 mm; adaxial surface purple, purple-veined; abaxial surface white, purple-veined; apex retuse; margin recurved; claw pale green, c. 1 mm long. Wings oblong, longer than keel, c. 4 × c. 1 mm; adaxial and abaxial surfaces white, distal area flushed purple, sometimes purple-veined; auricle rounded, white, c. 0.3 × c. 0.3 mm; claw pale green, c. 1 mm long. Keel c. 4 × c. 1.5 mm; distal area of adaxial and abaxial surfaces purple, central area white, and proximal area pale green;auricle rounded, white, c. 0.25 mm long; claw pale green, c. 2 mm long. Stamens

Fig. 3.11 *Carmichaelia compacta*, Nevis Bluff, Kawarau River gorge, Otago.

3-3.5 mm long; lower filaments connate for c. ⅞ length and with outside filaments free for 0.3-0.5 mm. Pistil exserted beyond stamens, c. 4 mm long; style with a ring of hairs below stigma; ovules 6-7. Pod obovate, broad at distal part, dorsally compressed, brown, pale grey, or straw-coloured, indehiscent, with inflated valves, 5-5.5 × 3-4 mm; beak on upper suture, slightly curved, stout, pungent, c. 1 mm long. Seeds oblong-reniform, 1(-2) per pod, light olive green or yellow-green with black mottling, 2-2.5 × 1.5-2 mm. Chromosome number unknown. FL Oct-Feb, FT Dec-Jul.

DISTRIBUTION AND HABITAT: Otago (Fig. 3.11, 3.24). Rock and debris slopes, rock outcrops, steep tussock grassland, and river gorges. The soils are derived from schist parent material. This species has a low water loss rate (Kissel et al. 1987), and is therefore suited to the dry conditions of Central Otago.

RECOGNITION (Fig. 3.4): *C. compacta*, *C. curta*, and *C. juncea* are recognised as a group by their dorsally compressed and indehiscent pods. *C. compacta* is distinguished from *C. curta* and *C. juncea* by its more upright and shrubby habit, green and densely placed cladodes, large obovate pods, large seed, and the lower filaments being connate for c. ⅞ of their length.

VARIATION: The growth habit varies from a low and spreading shrub which is broader than tall to an upright shrub of equal height and breadth. The infraspecific epithet *procumbens* was applied by Simpson (1945) to plants with a low and spreading growth habit, but this I regard as part of the natural variation of the species.

REPRESENTATIVE SPECIMENS: OTAGO: Cromwell Gorge, *H. H. Allan*, 13 Oct 1944, CHR 45854; Alexandra, *A. Wall*, Nov 1925, CHR 332014; between Alexandra and Omakau, *G. Simpson & J. S. Thomson 80*, Nov 1938, CHR 45903; Lindis Pass, *H. H. Allan*, 15 Dec 1948, CHR 107885; Cromwell, *M. J. A. Simpson 7664*, 17 Mar 1975, CHR 274191b; Gorge Creek, *A. Whitaker*, 3 Dec 1985, CHR 420042; Clyde, *A. W. Purdie*, 12 Dec 1985, CHR 421350; Kawarau Gorge, *G. Brownlie 980*, 25 Jan 1970, CHR 344757; Kawarau Gorge, *R. Powell*, Jan 1974, CHR 357994.

ETYMOLOGY: The specific epithet *compacta* probably refers to the closely placed

cladodes which are characteristic of this species.

ILLUSTRATION: Eagle (1982, fig. 90).

CONSERVATION STATUS: Rare. Plants are generally in small and often isolated populations of between 5 and c. 100 individuals. Populations at Nevis Bluff and at the northern end of the Cromwell Gorge number about 100 plants each, but there is an absence of seedlings and young plants. Browsing by sheep, goats, hares, and rabbits is likely to be preventing regeneration and causing early senescence of older plants, especially at the Nevis Bluff site. Field work in parts of the Kawarau Gorge that are of difficult access may locate additional populations. The classification of rare by Cameron et al. (1993) is supported.

6. ***Carmichaelia corrugata*** Colenso, *Trans. & Proc. New Zealand Inst. 15*, 320-321 (1883)

DESCRIPTION (Fig. 3.4): Dwarf, rhizomatous shrub, up to (20-)40-60(-80) mm × 1 m, forming a dense mat or tufts of cladodes. Rhizomes becoming increasingly stout and woody with age, 5-200(-400) × (1-)2-3.5(-5) mm. Cladodes linear, striate, compressed, erect, yellow-green to orange-green, glabrous, (20-)40-60(-70) × 1.5-3(-3.5) mm; apex subacute to obtuse, yellow to yellow-green; leaf nodes (2-)4-8(-12). Leaves simple, broad-obovate to broad-elliptic, fleshy, entire, green, present on seedlings and absent on mature plants, 5.5-8 × 3-5 mm; adaxial and abaxial surfaces with scattered hairs; apex emarginate to retuse; base cuneate to narrow-obtuse; petiole sparsely hairy, 2-2.5 mm long. Leaves on cladodes reduced to a scale, triangular, glabrous, 0.6-1.5 × 0.8-1.4 mm; apex acute. Stipules free, triangular, 0.6-1.1 × 0.6-1.2 mm; adaxial surface glabrous; abaxial surface hairy when young, glabrous at maturity; apex acute to sub-acute; margin hairy. Inflorescence a raceme, 1 per node, with (1-)2 flowers. Peduncle glabrous or sparsely hairy, green, 5-15 mm long. Bracts triangular, glabrous, pale green, 0.5-1 mm long; apex obtuse; margin hairy. Pedicel glabrous or hairy, pale green, 3-7.5 mm long. Bracteoles at top of pedicel, triangular, glabrous, green and often flushed red, c. 0.2 × c. 0.2 mm; margin hairy; apex acute. Calyx campanulate, c. 2.5 × c. 2.5 mm; inner surface

glabrous, green; outer surface glabrous or sparsely hairy, green. Calyx lobes triangular, flushed red, c. 0.5 mm long; apex acute; margin hairy or glabrous. Bud green. Standard obovate, patent, 8-10 × 6-8 mm; adaxial surface central area purple, margin white, sometimes purple-green veined; abaxial surface green, margin cream-green, sometimes purple-green veined; apex retuse; claw pale green, c. 1.5 mm long. Wings oblong, shorter than keel, 5-6.5 × c. 2 mm; adaxial surface distal area purple, proximal area green; abaxial surface white, sometimes purple-veined; auricle triangular, pale green, apex obtuse, c. 1.25 mm long; claw pale green, c. 1.5 mm long. Keel 6-8 × 2.5-3 mm; distal area of adaxial surface purple, proximal area pale green; distal area of abaxial surface purple-green, proximal area pale green; auricle triangular, pale green, with obtuse apex, c. 0.75 mm long; claw pale green, 2-2.5 mm long. Stamens 7.5-9 mm long; lower filaments connate for c. ⅔ length and outside filaments free for 1.5-2.5 mm. Pistil exserted beyond stamens, c. 10 mm long; style with a ring of hairs below stigma, and sometimes a few scattered hairs on adaxial surface; ovules 9-11. Pod elliptic-oblong, laterally compressed, weakly falcate, black, brown, or grey, 7.5-13(-15) × 3-4 mm; one valve partially dehiscent from base; beak on adaxial suture, slightly upturned, stout, pungent, 1.5-2 mm long. Seeds oblong-reniform, (2)-4-6-(9) per pod, black, brown, tan, or olive green, 1.2-2 × 1-1.5 mm. Chromosome number $2n = 96$ (Dawson 1989). FL Oct-Feb(-May), FT Nov-Jun.

DISTRIBUTION AND HABITAT (Fig. 3.24): Marlborough, Canterbury, and Otago. A single collection was made in 1915 from Mt Herbert, Banks Peninsula (CHR 45841); there are no modern collections from there, and a recent botanical survey of Banks Peninsula did not locate it (H. D. Wilson, pers. comm. Nov. 1993). Gravel and sand soils, stone and gravel ridges and terraces, dry sandy hummocks on terraces, river beds, and disturbed sites.

RECOGNITION (Fig. 3.4): *C. corrugata* is a dwarf rhizomatous shrub, and is distinguished from *C. uniflora* by its larger diameter rhizome; partially dehiscent pod; cladodes which are broader, more robust, often longer, and a yellow-green or orange-green colour; and usually two-flowered inflorescence.

VARIATION (Fig. 3.4): Cladode size and shape is variable: plants from Marlborough

often have longer and slightly narrower cladodes than those from Canterbury; and plants from Central Otago are a similar length but slightly narrower than those from Canterbury.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Awatere Valley, *J. H. McMahon*, Dec 1926, CHR 332249; Branch R., *A. P. Druce*, May 1974, CHR 273176; Corries Gully, Awatere Valley, *G. Simpson & J. S. Thomson no. 268*, CHR 54271; CANTERBURY: Christchurch, *A. J. Healy 54/459*, 25 Nov 1954, CHR 90115; Ashburton, *H. H. Allan*, 3 Dec 1918, CHR 11800; Lake Heron, *M. J. A. Simpson 5896*, 11 Feb 1970, CHR 204850; Wakanui Beach, *R. Mason 10684*, 24 Nov 1967, CHR 167372; Amberly Beach, *B. Molloy*, 15 Dec 1971, CHR 386233; Harper River, *B. H. Macmillan 71/3*, 3 Jan 1971; Hurunui River, *A. J. Healy*, 14 Dec 1943, CHR 41310; NE Lowry Peaks Range, *A. J. Healy*, 20 Dec 1946, CHR 51527; OTAGO: Kyeburn Diggings, *G. Simpson*, 2 Feb 1938, CHR 215429; Waitaki Valley, *G. Simpson*, Dec 1938, CHR 54267; Central Otago, *W. A. Thomson*, Jan 1917, CHR 331944; Maniototo Plain, *D. Petrie*, Jan 1892, CHR 331945; SOUTHLAND: Oreti River, *V. D. Zotov*, 17 Jan 1938, CHR 20583.

ETYMOLOGY: The specific epithet *corrugata* is Latin for corrugated, and refers to the pod of the type specimens being corrugated on the lower suture (Colenso 1883).

ILLUSTRATION: Eagle (1982, fig. 95)

CONSERVATION STATUS: Not threatened.

7. ***Carmichaelia curta*** Petrie, *Trans. & Proc. New Zealand Inst. 25*, 271-272 (1893)

≡ *Huttonella curta* (Petrie) Kirk, *Stud. fl. New Zealand,* 116 (1899).

= *C. curta* var. *glabra* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 282 (1945).

= *C. diffusa* Petrie, *Trans. & Proc. New Zealand Inst. 25*, 272 (1893).

DESCRIPTION (Fig. 3.4, 3.12): Spreading, sprawling, sparsely branched shrub up to 0.5-1 × 1-2(-2.5) m broad; in disturbed habitats frequently suckering and forming patches up to 0.25 m tall and 1-1.5 m broad. Branches slender, decumbent, spreading, occasionally erect, arching and sprawling outwards, 10-20 mm × 0.5-1.2 m. Cladodes linear, striate, slender, subterete to terete, olive green to brown-green, covered with purplish bloom when young, often brown or bronze in winter, becoming glabrous with age, 150-450 × 2-2.5 mm; leaf nodes 9-22. Leaves 1-7-foliolate, fleshy; adaxial surfaces mottled grey-green or brown-green, hairy; abaxial surfaces pale green, hairy; apex emarginate to retuse; base cuneate to obtuse; margin sparsely hairy. Single or terminal leaflet broad-elliptic to ovate, 5-12 × 3-7 mm. Lateral leaflets broad-elliptic, ovate, or obovate, 3-4 × 1.75-2.5 mm; petiole hairy, 10-12 mm long; petiolule glabrous, 0.1-0.3 mm long. Leaves on cladodes reduced to a scale, triangular, glabrous, c. 2 mm long; apex acute. Stipules free, triangular to narrow-triangular, hairy or glabrous, 1.0-1.2 × c. 1.0 mm; apex acute; margin hairy or glabrous. Inflorescence a raceme, 1(-2) per node, each with 9-11 flowers. Peduncle glabrous, covered with purplish bloom when young, 15-20 mm long. Bracts narrow-triangular, glabrous, c. 1 mm long; apex acute, with a tuft of hairs; margin sparsely hairy. Pedicel glabrous, reddish in colour, 2-3 mm long. Bracteoles at base of receptacle, narrow-triangular, flushed with red, 0.25-0.5 mm long; apex acute, with tuft of hairs; margin sparsely hairy. Calyx campanulate, 2.5-3 × c. 2 mm; inner and outer surfaces glabrous, green, usually flushed with red. Calyx lobes triangular, flushed red, c. 0.5 mm long; apex acute; margin hairy. Bud purple or white. Standard obovate, spreading above wings and keel, 3-4 × 3-4 mm; distal and central areas of adaxial and abaxial surfaces with purple blotch, proximal area pale green, sometimes purple-veined; apex retuse; margins white and recurved; claw pale green, c. 1.5 mm long. Wings broad-oblong, longer than keel, 3.5-4 × 1.5-2 mm; distal and central areas of adaxial and abaxial surfaces white, with proximal area pale green, sometimes purple-veined; auricle rounded, pale green, c. 0.25 mm long; claw pale green, 1-1.25 mm long. Keel 3.5-4.5 × c. 1.5 mm; distal area of adaxial and abaxial surfaces purple, central area white, proximal area pale green; auricle rounded, white, c. 0.25 mm long; claw pale green, c. 2 mm long. Stamens 3-4 mm long; lower filaments almost fully connate - alternate anthers subsessile and with free parts of filaments 0.2 mm long. Pistil similar length to

stamens, c. 4 mm long; style with a ring of hairs below stigma; ovules 5-7(-8). Pod short-obovate or broad-elliptic, occasionally almost orbicular, dorsally compressed, valves inflated, brown or straw-coloured, indehiscent, 4-5.5 × 2-2.5 mm; beak on adaxial suture, straight or only slightly curved, stout, pungent, 1-2(-2.5) mm long. Seeds oblong-reniform, 1-2 per pod, olive green or orange-brown with black mottling, 1.5-2 × 1.25-1.5 mm. Chromosome number $2n = 32$ (Dawson 1995). FL Oct-Feb(-Jul), FT Jan-Aug.

DISTRIBUTION AND HABITAT (Fig. 3.24): Otago and South-Canterbury. Rocky outcrops and river terraces. Often present on disturbed sites such as roadside cuttings.

RECOGNITION (Fig. 3.4): *C. curta*, *C. compacta*, and *C. juncea* are recognised as a group by their dorsally compressed and indehiscent pods. *C. curta* is distinguished from *C. compacta* and *C. juncea* by its spreading and sprawling open habit; sparsely placed and slender cladodes with purplish bloom when young; short-obovate or broad-elliptic, occasionally almost orbicular pod; intermediate seed size; and having the lower filaments almost fully connate, with alternate anthers ± sessile and with the filament 0.2 mm long.

VARIATION: Simpson (1945) provided the infraspecific epithet *glabra* for plants with a glabrous ovary and cladodes. Plants with these characters occur alongside plants that are of various degrees of hairiness, and this variation is found throughout the range of *C. curta*.

REPRESENTATIVE SPECIMENS: OTAGO: Kurow, *G. Simpson 34*, Dec 1939, CHR 213027B; Duntroon, *H. H. Allan*, 16 Aug 1937, CHR 18626; Waitaki Dam, *G. Simpson 34*, CHR 45905A; Lake Aviemore, *P. N. Johnson*, 2 Jul 1980, CHR 363670; Eweburn, Maniototo Co., *H. J. Matthews*, 1908, CHR 11827; Omarama, *I. A. McNeur*, 5 Jan 1958, CHR 96702.

ETYMOLOGY: The specific epithet *curta* means short or shortened; Petrie did not specify what this referred to when he described the species. Eagle (1982) suggests it refers to the short pod.

Fig. 3.12 *Carmichaelia curta*, Falls Dam, Otago.

ILLUSTRATION: Eagle (1982, fig. 89).

CONSERVATION STATUS: Rare. In the Waitaki River valley the river terrace habitat has been extensively modified by agricultural practices, and *C. curta* is often subjected to browsing and competition from pasture grasses and weeds. Plants adapt to these pressures with a suckering growth habit, but opportunities for seedling germination and establishment are limited. Populations on rock outcrops at Deep Stream (B. P. J. Molloy, pers. comm. Jan. 1994), Parsons Rock, and Falls Dam are not subjected to agricultural pressures. However, these sites are small and the number of plants at each is few. *C. curta* is often present on disturbed areas, such as roadside cuttings, and grows reasonably well in the absence of browsing, pasture plants, and weeds. The classification of rare by Cameron et al. (1993) is supported.

8. *Carmichaelia hollowayi* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 277 (1945)

DESCRIPTION (Fig. 3.5, 3.13): Dwarf shrub, with low-spreading and sprawling habit, frequently suckering, up to 0.5 × 1(–2) m. Branches 10–30 mm diameter, stout, horizontal, spreading, sometimes erect. Cladodes 50–80(–100) × 3–5 mm, erect to spreading, linear, striate, plano-convex, rarely terete, yellow-green to green, hairy when young, becoming glabrous when mature, apex obtuse and yellow-green; leaf nodes 5–10. Leaves simple, present on seedlings and sometimes on adults; lamina 4.5–12.5 × 1.8–4.5 mm, obovate to oblanceolate, fleshy, green and usually with several white blotches on adaxial surface, adaxial and abaxial surfaces with scattered hairs, apex retuse, base attenuate; petiole < 0.5 mm, glabrous, pale green. Leaves on cladodes reduced to scales, < 1 mm long, broad-triangular to triangular, hairy to sparsely hairy, apex subacute. Stipules c. 1 × c. 0.5 mm, free, broad-triangular, hairy. Inflorescence a raceme, (1–)2–3 per node, each with 2–6(–8) flowers. Peduncle 5–10 mm long, hairy, green. Bracts < 1 mm long, triangular, hairy on abaxial surface when young but glabrous at maturity, apex acute to subacute, margin hairy. Pedicel 1.5–2 mm long, hairy, green. Bracteoles 0.2–0.3 mm long, on upper part of pedicel or on receptacle, hairy on abaxial surface, sometimes with glands. Calyx 2.5–3 × c. 2 mm, campanulate,

green, outer surface hairy. Calyx lobes 0.4–0.6 mm long, triangular, green and usually flushed red, inner surface glabrous or hairy, appressed to corolla, apex subacute. Standard 7–8 × 7–8 mm, broad-orbicular, patent, positioned in central part of keel, keeled, apex emarginate; central area of inner surface purple or red-purple, margins white, usually purple-veined; outer surface white; claw c. 2.5 mm long, green. Wings 5.5–6.5 × 2.5–3 mm, oblong, broad in distal part, longer than keel, apex broad, obtuse to truncate; inner and outer surfaces white, usually purple-veined; auricle 0.4–0.7 mm long, triangular, pale green; claw 1.6–1.8 mm long, pale green. Keel c. 5 × c. 3.5 mm; distal part of inner surface purple, proximal part white or pale green; outer surface white and purple-veined; auricle c. 1 mm long, triangular, pale green, apex obtuse to subacute; claw c. 2 mm long, pale green. Stamens 4–5 mm long; dorsal filaments connate for c. three-quarters of length, outer stamens free for c. 1 mm. Pistil 4–5 mm long, similar in length to stamens, glabrous; ovules 5–8. Pods 8–11 × 4.8–6 mm, broad-elliptic, laterally compressed, usually drooping, light grey to yellow-brown, both valves dehiscent in proximal part, abruptly narrowed to beak; beak 1.5–2 mm long, in a central apical position, stout, more-or-less triangular, pungent-tipped. Seeds 2.5–2.9 × 2.4–2.6 mm, reniform, 1(–2) per pod, yellow-green or green with black mottling. Chromosome number $2n = 32$ (Dawson 1995). FL Nov–Dec, FT Jan–May.

DISTRIBUTION AND HABITATS (Fig. 3.13, 3.23): *Carmichaelia hollowayi* is an obligate calcicole restricted to Otekaike limestone (Gage 1957; Uttley 1920) on the south side of the Waitaki River valley, between Duntroon and the Waitaki Dam, Otago. It usually occurs on debris-mantled slopes, flat planar tops, along the exposed top edge of the scarp face, and less frequently on ledges and at the base of the scarp face. This limestone was laid down during the Oligocene (Gage 1957), and has been exposed at this locality for at least 1 million years (D. Lewis pers. comm. Feb 1995).

RECOGNITION (Fig. 3.5): *Carmichaelia hollowayi* is recognised by the pod, which is conspicuously laterally compressed by having very flat valves, and by the cladode apex, which is usually obtuse and rounded and not sharp-tipped as in the Waitaki River valley and Mackenzie Basin forms of *C. petriei* and *C. australis*. *Carmichaelia hollowayi* could be confused with prostrate, low-growing, rhizomatous and suckering forms of *C. petriei*, which are common in the Waitaki River valley, but these occur on river terraces

and fans and not in the vicinity of *C. hollowayi.*

REPRESENTATIVE SPECIMENS: OTAGO: Mt St Mary near Duntroon, *G. Simpson*, Dec 1939, CHR 213032; Awahokomo Creek, Waitaki Valley, *P. N. Johnson*, 7 May 1992, CHR 475382; Gards Road, Waitaki Valley, *P. B. Heenan*, 3 Apr 1995, CHR 496601; above Maori petroglyphs, west of Duntroon, *P. B.Heenan*, 3 Apr 1995, CHR 496602.

ETYMOLOGY: Named after the Rev. J. E. Holloway (1881–1945) who first collected plants from the Waitaki Valley, Otago.

ILLUSTRATION: Eagle (1982, fig. 92).

CONSERVATION STATUS: *Carmichaelia hollowayi* is ecologically and geographically restricted, being known from only three outcrops of Otekaike limestone in North Otago. On each of these outcrops plants are few, numbering only 3, 12, and about 45 when last counted. No seedlings or young plants have been seen in the wild, and at each site introduced pasture grasses and weeds are strong competitors with *C. hollowayi.* The small size of the three known populations, particularly those with only 3 and 12 individuals, suggests that this plant could be subject to decline should pressures on the habitat dramatically change. Cameron et al. (1993) classified the plant as rare and Cameron et al. (1995) as "Taxonomically indeterminate, Rare." As the populations with only 3 and 12 plants have suffered extensive habitat modification and destruction, and the third population has few young plants and seedlings, it is recommended that *C. hollowayi* be ranked as endangered (P. J. de Lange pers. comm).

DISCUSSION: *Carmichaelia hollowayi* is one of three species of New Zealand broom which grow exclusively on base-rich substrates. In eastern Marlborough *Carmichaelia astonii* occurs on Amuri limestone (Heenan 1995a) and *Notospartium glabrescens* occurs on Cretaceous and Tertiary mudstone, sandstone, and limestone.

Fig. 3.13 *Carmichaelia hollowayi*, Awahokomo Valley, Waitaki River valley, Otago.

9. ***Carmichaelia juncea*** Hook.f., *Fl. nov.-zel.* 1, 51 (1852)

= *C. prona* Kirk, *Trans. & Proc. New Zealand Inst. 27*, 350 (1895) ≡ *Huttonella prona* (Kirk) Kirk, *Stud. fl. New Zealand*, 116 (1899).

= *C. fieldii* Cockayne, *Trans. & Proc. New Zealand Inst. 50*, 163-64 (1918).

= *C. lacustris* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 282-283 (1945).

= *C. nigrans* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 285-286 (1945).

= *C. nigrans* var. *tenuis* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 286 (1945).

= *C. floribunda* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 283 (1945).

DESCRIPTION (Fig. 3.4, 3.14): Prostrate, sprawling shrub, up to 0.2 × 1.5 m, forming a flat spreading mat. Branches up to 0.8 m long, procumbent. Cladodes linear, striate, compressed, green to light brown, sparsely covered with hairs, prostrate and ascending, 55-160 × 1.5-2 mm; apex subacute, green or light brown; leaf nodes 8-15. Leaves 1-3(-5)-foliolate, fleshy; adaxial surface mottled brown, brown-green or green; abaxial surface green; apex emarginate to retuse; base cuneate to obtuse; margin glabrous to sparsely hairy, sometimes partially sinuate. Single or terminal leaflet oblong, 5.5-14 × 2-4 mm; adaxial and abaxial surfaces hairy. Lateral leaflets obovate, 3-5 × 1-2.5 mm; adaxial and abaxial surfaces glabrous to sparsely hairy; petiole hairy, 4-8 mm long; petiolule glabrous, 0.1-0.3 mm long. Leaves on cladodes reduced to a scale, triangular, glabrous, < 1 mm long; apex acute. Stipules free, broad-triangular, 0.5-0.8 × c. 1 mm; apex subacute; margin hairy; thinly herbaceous at first but becoming dry and membranous. Inflorescence a raceme, 1(-2) per node, each with 4-6 flowers. Peduncle hairy, green, 2-4 mm long. Bracts triangular, glabrous, < 0.5 mm long; apex acute; margin hairy. Pedicel hairy, pale green and usually flushed red, 1-1.5 mm long. Bracteoles on pedicel, triangular, glabrous, 0.3-0.4 mm long; apex acute; margin hairy. Calyx campanulate, c. 1.5 × c. 1.25 mm; inner surface glabrous, green, occasionally

flushed red; outer surface glabrous, green. Calyx lobes broad-triangular to triangular, c. 0.1 mm long; apex subacute, often flushed red; margin hairy. Bud pale green. Standard obovate, patent, 4-5 × 4-5 mm; distal and central areas of adaxial surface purple, margins and proximal area white, sometimes purple-veined; distal and central areas of abaxial surface white, proximal area green, sometimes purple-veined; apex retuse; margins recurved; claw pale green but becoming pale green, c. 1.5 mm long. Wings oblong, longer than keel, 3.5-4 × 1-1.5 mm; adaxial and abaxial surfaces white, sometimes purple-veined; auricle rounded, pale green, < 0.5 mm long; claw pale green, 1-1.5 mm long. Keel c. 4.5 × c. 1.5 mm; distal area of adaxial surface purple, white in central and proximal areas; abaxial surface white, sometimes purple-veined; auricle rounded, white, c. 0.15 mm long; claw pale green, 1.5-2 mm long. Stamens c. 3.5 mm long; lower filaments connate for c. ⅔ of length and with outside filaments free for c. 1 mm. Pistil similar length to stamens, 3-3.5 mm long; style with a ring of hairs below stigma; ovules 4-10. Pod oblong, weakly dorsally compressed, valves inflated, dark grey-black, indehiscent, rarely weakly dehiscent at proximal end, 3.5-6 × 1.75-2 mm; beak on adaxial suture, slightly curved, stout, pungent, 0.25-0.5 mm long. Seeds oblong-reniform, (1-)2-4(-6) per pod, brick red, orange, olive green, or green-yellow, often with black mottling, 1.25-1.5 × c. 1 mm. Chromosome number $2n = 32$ (Dawson 1989). FL Oct-Jan, FT Nov-Mar.

DISTRIBUTION AND HABITAT (Fig. 3.15, 3.24): Hawke's Bay, Nelson, Westland, Canterbury, and Otago. Wardle (1975) recorded *C. nigrans* from below the Franz Josef glacier terminal face and from Welcome Flat, Copland River. Cockayne (1907) reported plants of *C. prona* growing at the Rakaia River mouth, but this is not supported by a herbarium voucher. Another prostrate species, *C. appressa*, is restricted to the nearby Kaitorete Spit and it is probable that this species once grew at the Rakaia River mouth. Cockayne may have misidentified the plants he saw as *C. prona* because of the similar prostrate growth habit.

The exact locality of Colenso's Hawke's Bay collection of *C. juncea* is unknown. Colenso's mission station in Hawke's Bay was at Waitangi (Bagnall & Peterson 1948), near the Ngaruroro River, which is the most likely habitat in the area. *C. juncea* joins the group of plants that are widespread in the South Island and with a disjunct population in the central North Island (for discussion see Wardle 1963, Burrows 1965,

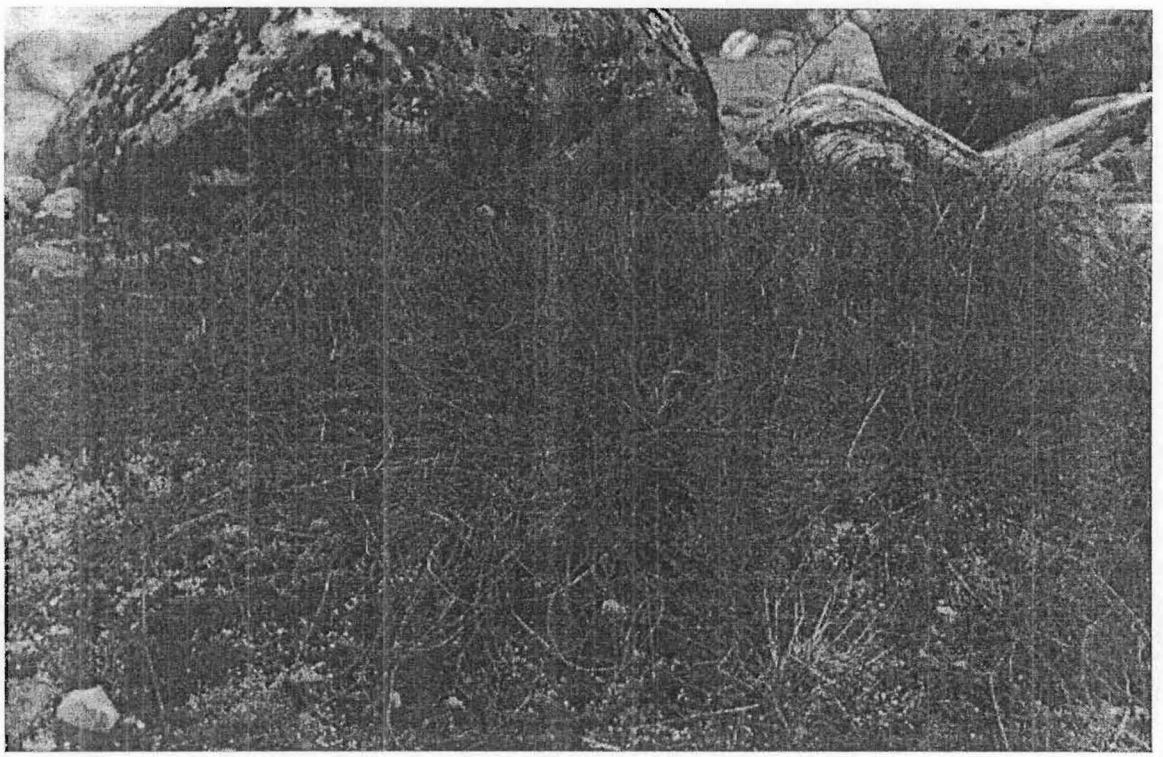


Fig. 3.14 *Carmichaelia juncea*, Fox River, Westland.

McGlone 1985, and Rogers 1989).

C. juncea occurs on stable but unconsolidated river bed gravels, flood bed margins, and stony, gravelly, sandy, and grassy edges of lakes where competition with other vegetation is limited. Not recorded from neighbouring, more advanced communities in Westland (Wardle 1977). Colenso's notes, under collection number 1845 in the list of plants he sent to W. J. Hooker, make reference to the habitat of *C. juncea* as "grows in beds!" This compares favourably with the known habitat preferences of extant populations of *C. juncea* in the South Island.

RECOGNITION (Fig. 3.4): *C. juncea*, *C. compacta*, and *C. curta* are recognised by their dorsally compressed and indehiscent pods. *C. juncea* is distinguished from *C. compacta* and *C. curta* by its prostrate and procumbent habit; short or long-oblong pod that is weakly dorsally compressed; the lower filaments connate for c. ⅔ of their length and

with the outside filaments free for c. 1 mm; and shorter inflorescences.

VARIATION (Fig. 3.4): Pod shape and the number of seeds per pod vary: plants from the west coast of the South Island have long, often dark-coloured pods, with (2-)4-6 seeds; plants from the central South Island and north-west Nelson have slightly smaller pods, are lighter in colour, and have 2-4(-6) seeds; and plants from Marlborough and North Island localities have short pods of a light tan colour with 1-2(-4) seeds.

REPRESENTATIVE SPECIMENS: NELSON: West Wanganui Inlet, *A. Wall*, Nov 1924, CHR 332006; Greenhills Stream, *D. R. Given 14072*, 29 Dec 1985, CHR 420378; WESTLAND: Waiho River, *A. Wall*, Jan 1924, CHR 332059; Cook River flats, *P. Wardle & I. K. Fryer*, 25 Jun 1967, CHR 166996; CANTERBURY: Lake Mary Mere, *G. Simpson & W. B. Brockie*, 27 Dec 1938, CHR 45812; OTAGO: Lake Manapouri, *H. J. Matthews*, Feb 1909, AK 209784.

ETYMOLOGY: The specific epithet *juncea* probably refers to the leafless and rush-like habit of this species.

ILLUSTRATION: Eagle (1982, fig. 82).

CONSERVATION STATUS: Endangered. This species once occurred over a large geographical area, but was probably never very common because of the specific habitat it occupies. It is now restricted to small and isolated populations in N. W. Nelson and on the west coast of the South Island. A recent collection from an island in the Fox River located only 25 plants (Buxton 1993).

The main threats today are continued habitat modification and competition from weed species and pasture grasses; browsing by hares and livestock; and modification of river systems from multi-channelled and braided river beds to single channels, with consequent loss of braid islands and cyclical creation of suitable habitat. Because extinction is likely if the above threats continue, this species is listed as endangered.

DISCUSSION: For what is accepted here as a single species, *C. juncea*, an extensive list of synonyms and considerable taxonomic uncertainty has resulted from each newly

discovered population being described as a new species or variety. As originally circumscribed, *C. juncea*, *C. floribunda*, and *C. nigrans* are each known only from the type collection; *C. prona* is extinct at the original localities, but plants are in cultivation; *C. lacustris* is known from three collections, but has not been collected in recent years; and *C. nigrans* var. *tenuis* and *C. fieldii* still occur in the general area of their type locality.

Several characters clearly indicate that *C. juncea* and its synonyms are conspecific. These include pod shape, seed size, stipule size and shape, inflorescence length and hairiness, placement of the bracteoles and lower filament fusion.

Kirk (1899) and Cheeseman (1925) noted that more than one species may have been included in *C. juncea*. Cockayne (1917) described vegetative and flowering specimens collected by Christensen from the Clarence River between Jacks and Jollies passes as "*Carmichaelia juncea* var." Cockayne did not examine pods, and his description refers to a low shrub, rather than a prostrate or procumbent plant which would be more typical of *C. juncea*. The herbarium specimen (WELT 26707) representing this collection and Cockayne's description are not consistent with *C. juncea* as described by Colenso. Allan (1961) treated *C. juncea* as *incertae sedis*.

Incertae sedis

Carmichaelia juncea Hook.f. var. γ *parviflora* Benth., in J. D. Hooker, *Fl. nov.-zel.* 1, 51 (1852). Described as "floribus minimus." Hooker (1864) and later authors make no mention of this variety and it appears to have been abandoned. No type specimens have been located, and this name is treated as *nomen dubium*.

Carmichaelia juncea Hook.f. var. β *Fl. nov.-zel.* 1, 51 (1852). Described as "legumine 2 lin. longo." This variety was not formally named and was not referred to by Hooker (1864) or subsequent authors.

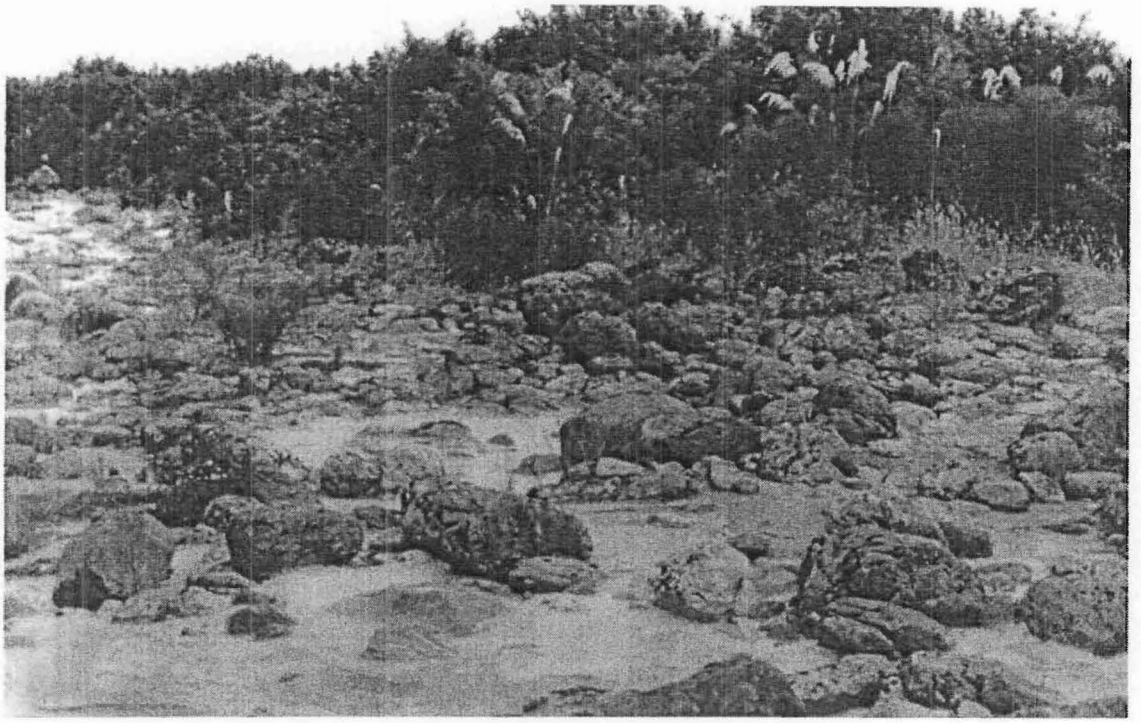


Fig. 3.15 *Carmichaelia juncea* habitat, Fox River, Westland.

10. *Carmichaelia kirkii* Hook.f., *Hooker's Icon. Pl. 14*, t. 1332 (1881)

= *C. kirkii* var. *strigosa* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 267 (1945).

= *C. gracilis* J.B.Armstr., *Trans. & Proc. New Zealand Inst. 13*, 336 (1881).

DESCRIPTION (Fig. 3.5, 3.16): Liana, up to 1–3 m tall, climbing, scrambling, and sprawling, or rarely a bushy shrub without support. Branches up to 40 mm diameter, ascending and spreading. Cladodes 70–350(–420) × 1.7–3 mm, spreading and often divaricate, linear, striate, terete, green, green-bronze, or bronze, hairy or glabrous, apex obtuse; leaf nodes 4–12. Leaves 1–5–foliolate, present on seedlings and usually on inner parts of adult plants, terminal leaflet larger; lamina 4.5–8 × 2.5–6 mm, obovate to broad-elliptic, fleshy, green or bronze-green, adaxial surface glabrous, abaxial surface

glabrous or with a few scattered hairs, apex emarginate, base cuneate; petiole 6–25 mm long, glabrous or hairy, green or brown-green; petiolule 0.5–0.9 mm long, glabrous, light green. Leaves on cladodes reduced to scales, < 0.6 mm long, broad-triangular, glabrous, apex subacute. Stipules 0.7–1 × 0.6–0.8 mm, free, triangular, adaxial surface glabrous, abaxial surface with few scattered hairs, apex subacute, margin hairy. Inflorescence a raceme, 1–2(–3) per node, each with (1–)2–5 flowers. Peduncle 2–6 mm long, glabrous to densely hairy, green or red. Bracts 0.5–1.2 mm long, triangular, sparsely hairy, apex obtuse or subacute, margin hairy. Pedicel 2.5–4 mm long, glabrous to densely hairy, green or red. Bracteoles c. 0.5 × c. 0.3 mm, narrow-triangular, on receptacle or lower part of pedicel, green or red, apex obtuse to subacute, margin hairy. Calyx 4–5 × c. 2 mm, campanulate, green and occasionally flushed red, outer surface glabrous or hairy. Calyx lobes 1.5–2.5 mm long, narrow-triangular, green and usually flushed red, inner surface densely hairy, apex acute; two ventral lobes appressed to base of standard, three dorsal lobes spreading away from keel. Standard 8–9 × 8.5–12 mm, orbicular or broad-obovate, patent, positioned in central part of keel, weakly keeled, margins recurved, apex emarginate or occasionally mucronulate; central part of inner surface red-purple, margins white, sometimes purple-veined; outer surface white with a darkened central part; claw 2–3 mm long, green. Wings 6–8 × 2.5–3.5 mm, oblong, shorter than keel, apex obtuse; outer surface white, proximal part pale green; inner surface sometimes purple-veined; auricle 1–1.5 mm long, triangular, white or flushed green; claw 2–2.5 mm long, pale green. Keel 8–9 × 3–3.5 mm, apex obtuse; distal part of inner surface red-purple, proximal part white or pale green; auricle c. 1 mm long, triangular, white or pale green; claw 3–4 mm long, pale green. Stamens 6.5–8.5 mm long; dorsal filaments connate for c. ¾ of length, outer stamens free for c. 2 mm. Pistil 8.5–10 mm long, exserted beyond stamens; style bearded on upper surface, ovary glabrous; ovules 8–10. Pods 12–18 × 4–5.8 mm, broad-elliptic, laterally compressed, spreading, dark brown, grey-brown, or yellow-brown, both valves partially dehiscent and remaining attached to lower replum; beak 3–6 mm long, on adaxial suture or in central apical position, stout, pungent-tipped. Seeds 2–3.5 × 1.7–2.5 mm, broad-elliptic, reniform, oblong-reniform or rounded, 2–5 per pod, off-white with black or dark purple mottling. Chromosome number $2n = 32$ (Slade 1953). FL Nov–Jan, FT Jan–Jun.

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia kirkii* occurs in small, local, and

often widely dispersed populations in Marlborough, Canterbury, and north Otago in the South Island. It grows among grey scrub communities of mainly divaricating shrubs which provide ideal support for its climbing habit. Although the precise habitat requirements for *C. kirkii* are not understood, this plant appears to favour mature scrub at the bottom of terrace risers, on the banks of gullies, or on toe slopes. Where support is not available it often grows as a dense clump or mound of tangled stems on the margins of scrub.

RECOGNITION: *Carmichaelia kirkii* is easily recognised as it is the only climbing *Carmichaelia*, the seeds are consistently and uniformly mottled off-white and black or dark purple, and the pod has a prominent, stout, and centrally placed beak.

VARIATION: The cladodes can be stout (c. 3 mm diameter) to slender (c. 1.7 mm diameter), glabrous to densely hairy, and green, brown-green, or red-purple in colour. These three cladode attributes vary throughout the range of the species, although a given population will usually exhibit only a single combination of the above character states. Attempts to correlate different combinations of the above cladode characters with distribution have been unsuccessful. Seed collected from Banks Peninsula has given rise to both hairy and glabrous plants (H. D. Wilson pers. comm.).

REPRESENTATIVE SPECIMENS: MARLBOROUGH: upper Tone, *P. A. Williams*, Jan 1984, CHR 405262b; CANTERBURY: Coopers Creek, *A. P. Druce*, May 1978, CHR 323502; New Brighton, *A. Wall*, Dec 1918, CHR 332057; Rakaia Island, *G. Simpson & R. T. Richards*, CHR 45773b; Poulter River, *G. Simpson*, AK 103150; Benmore Range, *P. N. Johnson*, 1 Jul 1980, CHR 363671; OTAGO: Deep Creek, Cardrona Valley, *A. W. Purdie*, 10 Dec 1985, CHR 421341; Dunback, *A. W. Purdie*, 13 Dec 1985, CHR 421347; Otepopo River, *G. Simpson*, CHR 457698.

ETYMOLOGY: The epithet *kirkii* commemorates T. Kirk (1829–98), who first collected the plant from Cardrona Valley, Otago.

ILLUSTRATIONS: Hooker (1881, pl. 1332), Eagle (1982, fig. 87), and Wilson & Galloway (1993, fig. 69).

CONSERVATION STATUS: *Carmichaelia kirkii* is known from small populations scattered throughout eastern and central areas of the South Island. However, it is uncommon and is known only from a few localities in Marlborough, Otago, and north and central Canterbury. In the general vicinity of the Benmere Range in south Canterbury a large number of collections have been made, but detailed field studies of these sites are needed to obtain a more accurate assessment of its conservation status. At some localities there are often only a few older plants, no seedlings or young plants, and the habitat is often significantly disturbed or modified. The habitats of *C. kirkii* are prone to regular anthropogenic disturbance, and the long-term survival of the plant is in doubt at some localities. Given the number of collections from the upper part of the Waitaki River valley, the classification of endangered by Cameron et al. (1993) and critical by Cameron et al. (1995) is probably an over-estimation of its rarity. Until field surveys are undertaken and the abundance of the species is better understood, a more realistic classification would be rare.

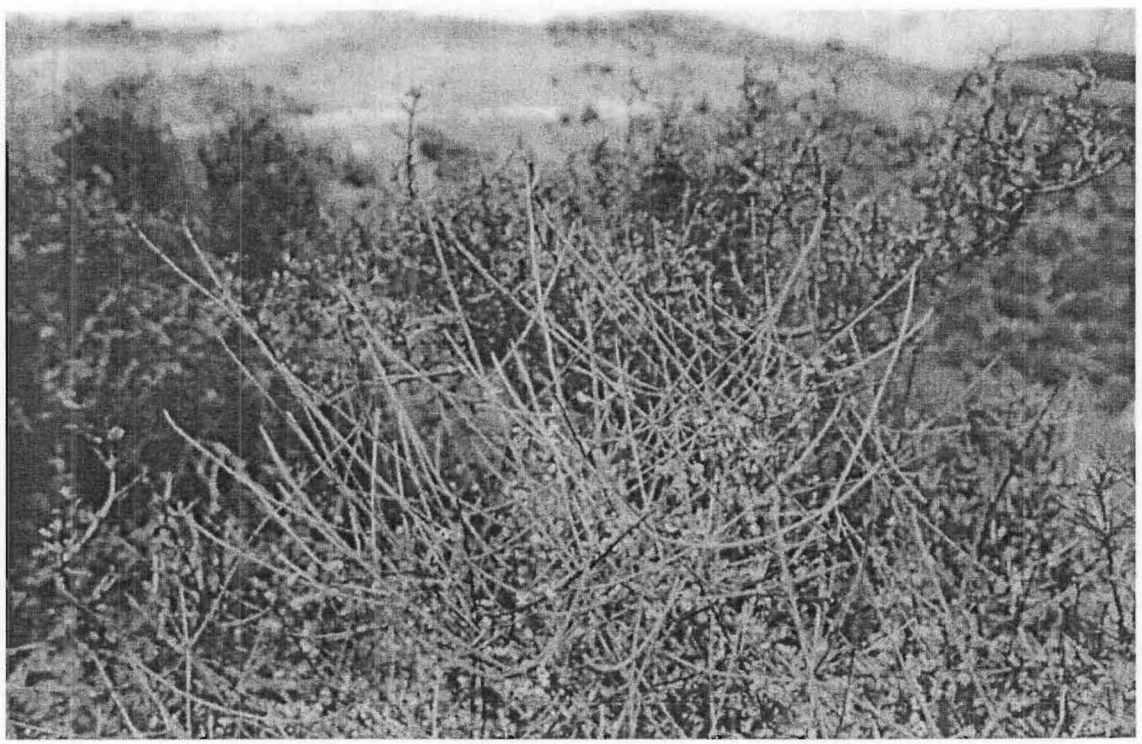


Fig. 3.16 *Carmichaelia kirkii*, Cluden Stream, Otago.

11. ***Carmichaelia monroi*** Hook.f., *Handb. N. Zeal. fl.*, 49 (1864)

= *C. monroi* var. *longecarinata* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 279 (1945).

DESCRIPTION (Fig. 3.4, 3.17): Dwarf, spreading shrub, up to 0.15(-0.25) × 0.4(-1) m broad. Branches stout, ascending and horizontal, 10-35 mm diameter. Cladodes linear, striate, compressed, erect to spreading, green to green-bronze, often hairy when young, glabrous at maturity, 22-40(-75) × (2-)3-5(-6) mm; apex obtuse, yellow, green, bronze, or red; leaf nodes 2-4. Leaves simple, oblanceolate, fleshy, green to green-bronze, present on seedlings and occasionally mature plants, 5-8 × 2-4.5 mm; adaxial and abaxial surfaces with scattered hairs; apex emarginate to retuse; base cuneate; petiole glabrous or sparsely hairy, 1.5-2 mm long. Leaves on cladodes reduced to a scale, broadly triangular, glabrous, 0.5-0.6 × 0.9-1.1 mm; apex obtuse. Stipules free, broad-triangular, 0.25-0.4 × 0.75-0.9 mm; adaxial surface glabrous; abaxial surface hairy, becoming glabrous with age; apex subacute; margin hairy. Inflorescence a raceme, 1-2 per node, each with (1-)2-3 flowers. Peduncle hairy, green, 6-8 mm long. Bracts triangular, glabrous, pale green to tan, < 0.5 mm long; apex acute; margin hairy. Pedicel hairy, pale green, 3-4 mm long. Bracteoles at base of calyx, sometimes absent, glabrous, < 0.4 mm long; apex subacute; margin hairy. Calyx campanulate, 2.5-3 × c. 2 mm; inner surface glabrous, green; outer surface hairy, green. Calyx lobes triangular, green and often flushed red, < 1 mm long; outer surface densely hairy; apex acute, often black; margin hairy. Standard obovate, patent when young, reflexed at maturity, positioned at proximal area of keel, keeled, 6-7 × 5-6 mm; distal and central areas of adaxial surface purple, proximal area pale green, margins white, sometimes purple-veined; distal and central area of abaxial surface white, proximal area pale green, sometimes purple-veined; apex retuse; margins recurved; claw pale green, c. 3 mm long. Wings oblong, shorter than keel, 7-8 × c. 2 mm; distal and central areas of adaxial surface purple, proximal area green; distal and central areas of abaxial surface white, proximal area pale green; auricle triangular, pale green, apex subacute, c. 1 mm long; claw pale green, c. 2 mm long. Keel 8.5-10 × 3-4 mm; distal and central areas of adaxial surface purple, proximal area pale green; auricle triangular, pale green, with subacute apex, c. 1.5 mm long; claw pale green, 3-3.5 mm long. Stamens 8.5-10 mm

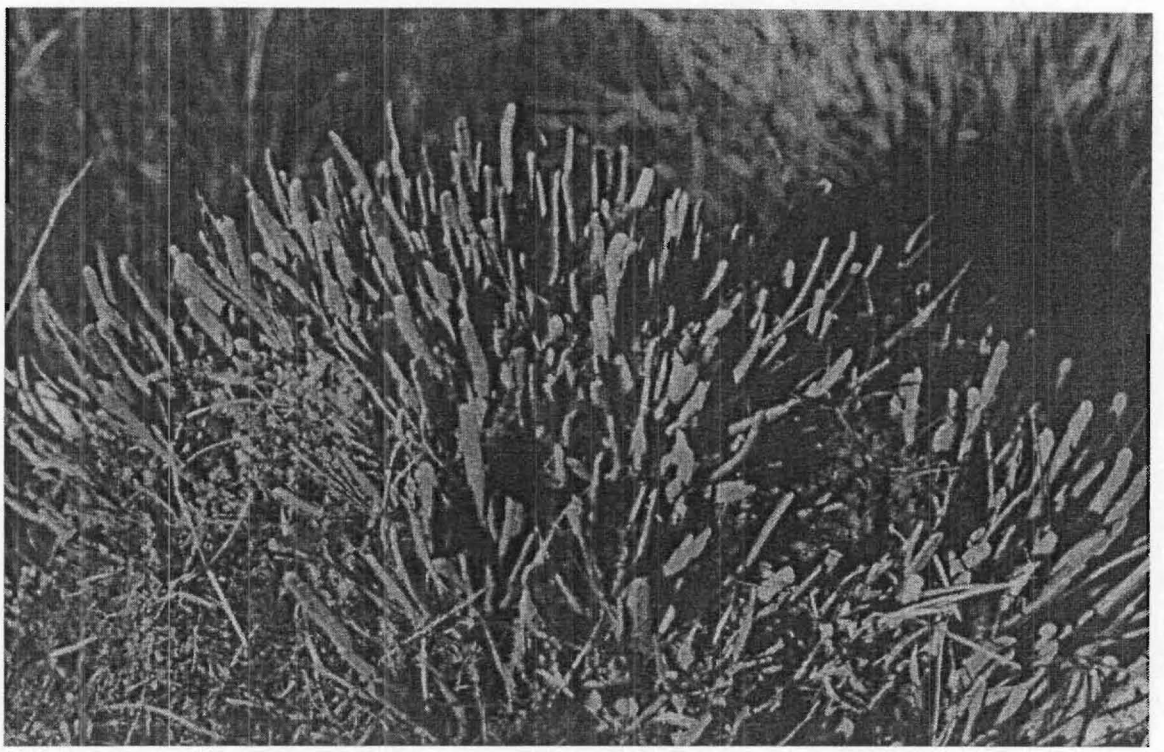


Fig. 3.17 *Carmichaelia monroi*, Porters Pass, Canterbury.

long; lower filaments connate for c. ⅔ length and outside filaments free for 2.5-3.5 mm. Pistil slightly exserted beyond stamens, 8.5-11 mm long; style bearded on upper surface; ovary weakly falcate, glabrous; ovules 11-12. Pod oblong or oblanceolate, laterally compressed, often weakly falcate, brown, dark brown, or black, usually indehiscent, 11-15 × 3.5-5.5 mm; beak on adaxial suture, stout, pungent, < 1 mm long. Seeds oblong-reniform, (3-)7-11 per pod, dull yellow or orange, brown-green, or olive green, often with black mottling, 2-2.5 × 1.5-2 mm. Chromosome number $2n = 32$ (Slade 1953; Dawson 1989). FL Nov-Jan, FT Dec-May.

DISTRIBUTION AND HABITAT (Fig. 3.24): Marlborough and Canterbury. Stable slopes, terraces, and braid islands. Often growing among loose rock, scree debris, and eroding soils at the interface between rock outcrops and unstable scree and the adjacent tussock and shrub vegetation. Limestone-derived soils at Castle Hill, Prebble Hill, and Flock

Hill, Canterbury.

RECOGNITION (Fig. 3.4): *C. monroi* is a dwarf shrub distinguished from the similar *C. astonii* and *C. vexillata* by its densely hairy calyx with short lobes, and the standard placed at the proximal area of the keel; from *C. astonii* by its smaller habit, cladodes, and flowers; and from *C. vexillata* by the triangular or broad-triangular stipules.

VARIATION: Plants from limestone at Castle Hill, Prebble Hill, and Flock Hill, in the Trelissick Basin, have much narrower cladodes than plants at nearby Porters Pass, Lake Lyndon, and Poulter River. Plants from an andesite protrusion at Stew Point have very robust, broad, and flattened cladodes; and plants from Bankside Reserve on the Canterbury plains have a more shrubby habit.

REPRESENTATIVE SPECIMENS: MARLBOROUGH: Barefell Pass, Awatere River, *J. Stevens*, 29 Nov 1972, CHR 243710; CANTERBURY: Mt Terako, *H. Talbot*, Dec 1948, CHR 391582; Lake Heron, *C. R. Mason*, 27 Jan 1985, CHR 419680; Porters Pass, *A. W. Purdie*, CHR 436416; Broken River, *G. Simpson*, CHR 59489; Bankside Reserve, *B. P. J. Molloy*, 12 Dec 1969, CHR 201478; Great Island, *B. Molloy*, 24 Nov 1971, CHR 386300; Dog Range, *K. F. O'Conner*, 26 Mar 1968, CHR 184359; Stew Pt N. Peel Ra., *A. P. Druce*, Mar 1985, CHR 401949; Waimakarari River, *W. B. Brockie*, CHR 54257.

ETYMOLOGY: The epithet *monroi* commemorates D. Monro (1813-1877).

ILLUSTRATION: Eagle (1982, fig. 91).

CONSERVATION STATUS: Not threatened.

12. *Carmichaelia nana* (Hook.f.) Hook.f., *Handb. N. Zeal. fl.*, 49 (1867)

≡ *C. australis* var. β *nana* Hook.f., *Fl. nov.-zel.*, 50 (1852).

= *C. enysii* Kirk, *Gard. Chron., n.s., 21*, 512 (1884).

= *C. enysii* var. *ambigua* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 269-270 (1945).

= *C. orbiculata* Colenso, *Trans. & Proc. New Zealand Inst. 22*, 459-460 (1890) ≡ *C. enysii* var. *orbiculata* (Colenso) Kirk, *Stud. fl. New Zealand*, 108 (1899).

DESCRIPTION (Fig. 3.4, 3.18): Dwarf, spreading shrub, 20-60 mm × 0.5 m, usually forming a dense mat of cladodes. Branches short, stout, often below ground level, 10-20 mm diameter. Cladodes linear, striate, compressed, usually erect and crowded, green or yellow-green, often hairy when young, glabrous at maturity, 10-30(-50) × 1.5-2(-4.5) mm; apex subacute, yellow, yellow-green, or red; leaf nodes 2-5(-7). Leaves simple, obovate to broad-oblanceolate, fleshy, green, only occasionally present on seedlings and absent on adults, 4-5 × 1-2 mm; adaxial and abaxial surfaces hairy; apex retuse to obtuse; base cuneate; margins hairy; petiole glabrous or hairy, c. 1 mm long. Leaves on cladodes reduced to a scale, narrow to broad-triangular, glabrous, < 1 mm long; apex subacute to obtuse. Stipules free, c. 0.5 × c. 0.25 mm; margin hairy. Inflorescence a raceme, 1-2 per node, each with (1-)2-3(-4) flowers. Peduncle glabrous to hairy, green, 3-4 mm long. Bracts triangular, glabrous, pale green becoming membranous, < 0.5 mm long; apex subacute to obtuse; margin hairy. Pedicel glabrous or hairy, pale green, 1-2 mm long. Bracteoles on pedicel, glabrous, < 0.5 mm long; apex acute; margin hairy. Calyx campanulate, green to green-yellow, 1.5-2 × 1-2 mm; inner surface glabrous; outer surface glabrous to sparsely hairy. Calyx lobes narrow- to broad-triangular, c. 0.5 mm long; apex subacute to obtuse, red to green; margin hairy or occasionally glabrous. Bud pale purple. Standard obovate, spreading horizontally above wings and keel, 4.5-6.5 × 4-5 mm; adaxial surface purple, with white margins and purple-veined; abaxial surface white, purple-veined; apex retuse; margin recurved; claw pale green, c. 1.25 mm long. Wings oblong, longer than keel, 3.5-5.5 × c. 1.25 mm; adaxial and abaxial surfaces white, flushed purple, sometimes purple-veined; auricle rounded, pale green or white, < 0.25 mm long; claw pale green, c. 2 mm long. Keel 4.5-5 × c. 1.25; distal area of adaxial and abaxial surfaces purple, white in central and proximal areas, sometimes purple-veined; auricle rounded, pale green or white, c. 0.25 mm long; claw pale green,

c. 2 mm long. Stamens 3.5-5 mm long; lower filaments connate for c. ½ length and with outside filaments free for 1.75-2.25 mm. Pistil exserted beyond stamens, 4-6 mm long; style glabrous or with few scattered hairs on adaxial surface; ovules (4-)7-8. Pod short- or broad-oblong, occasionally broad-elliptic or ovate, laterally compressed, brown, black, or yellow-green, one valve partially dehiscent from upper replum, other valve usually indehiscent or only weakly dehiscent, 5-7 × 4.5-5.5 mm; beak in a central apical position, straight or slightly curved, 1-3 mm long. Seeds oblong-reniform, 1-3 per pod, yellow, yellow-green, green, or black, occasionally with green or black mottling, 2.5-3 × 1.75-2 mm. Chromosome number $2n = 32$ (Dawson 1989). FL Nov-Feb, FT Jan-May.

DISTRIBUTION AND HABITAT (Fig. 3.24): Central North Island, Marlborough, Canterbury and Otago. Usually occurs on stable but unconsolidated alluvial river beds and braid islands, river terraces, moraines, and shingle slopes.

RECOGNITION (Fig. 3.4): *C. nana* is distinguished from the other dwarf *Carmichaelia* species by its smaller flowers, usually short-oblong or broad-oblong pod, and having one valve partially dehiscent from the upper replum.

VARIATION (Fig. 3.4): Cladode size varies within and between populations of *C. nana*. At one extreme in the central North Island and in the Waitaki Valley of the South Island the cladodes are generally robust and the plants have an open and spreading habit. The robust North Island plants have been previously named as *C. orbiculata*. In other areas, such as the catchment at the headwaters of the Ashburton River, the cladodes are smaller, densely crowded, and more erect. Plants in a given population are usually variable, and the largest cladodes at one locality can often be similar to the smallest size at another. Simpson's variety *ambigua* represents a form of intermediate cladode size, which is within the range of natural variation.

Plants in the Waitaki River valley appear to be rhizomatous, but this is a result of plants collecting wind-blown loess which builds up around them, burying the branches and cladodes.

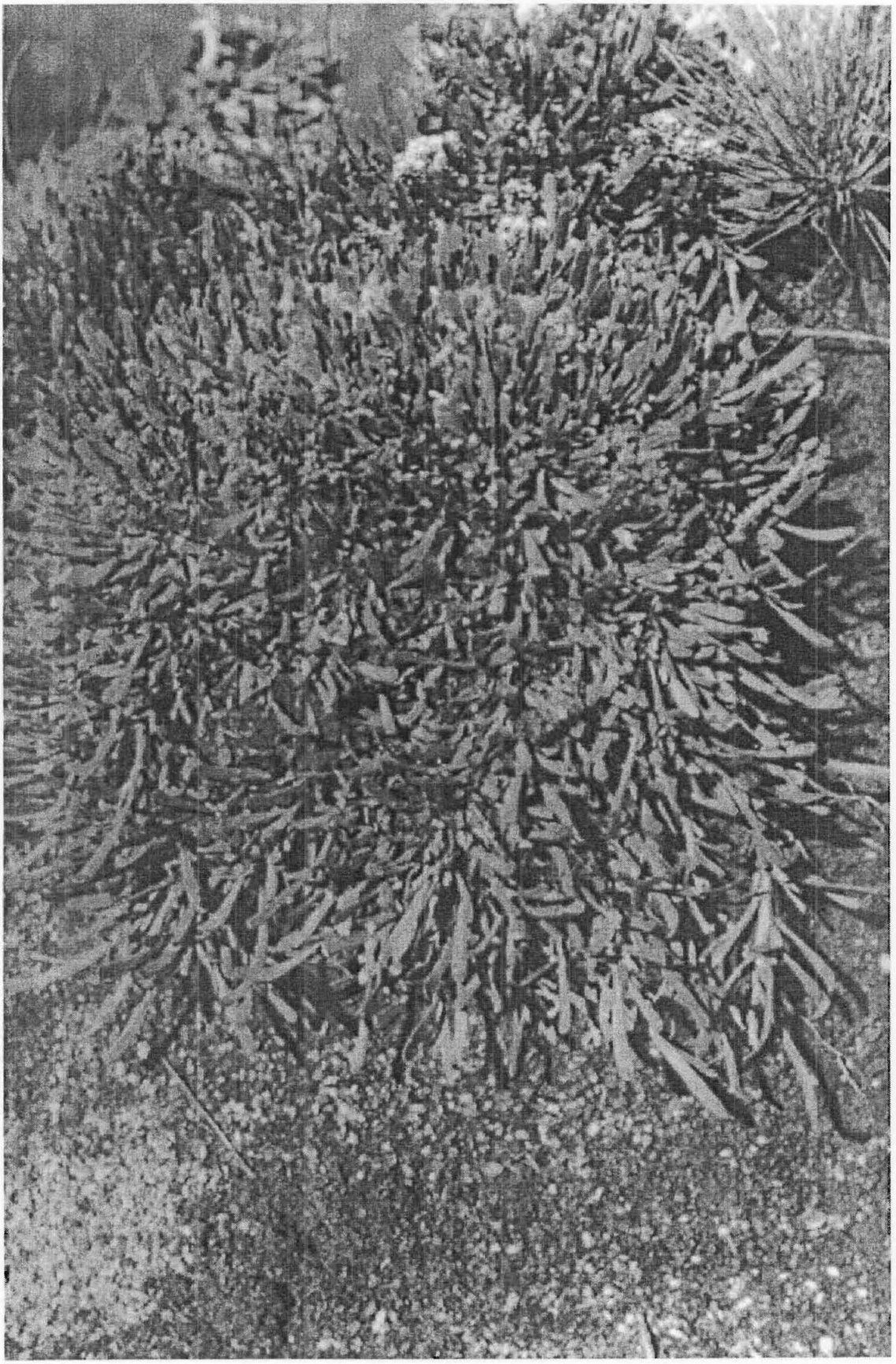


Fig. 3.18 *Carmichaelia nana*, Rangipo Desert, central North Island.

REPRESENTATIVE SPECIMENS: NORTH ISLAND: Ruapehu, *A. P. Druce*, 8 Mar 1959, CHR 141853; Desert Rd., *A. P. Druce*, Apr 1978, CHR 324245; Mt Tongariro, *E. S. West*, CHR 213068B; Kaimanawa Mts, *A. P. Druce*, Dec 1946, CHR 116324; MARLBOROUGH: Robinson's Stream, Awatere Valley, *L. B. Moore*, 21 Feb 1970, CHR 201761; CANTERBURY: Ashburton Gorge, *K. F. O'Conner*, 3 Mar 1969, CHR 194917; Spider Lakes, *P. N. Johnson*, 27 Feb 1979, CHR 320278; MacKenzie Pass, *J. Smith-Dodsworth & C. Jones*, CHR 462571; Broken River basin, *G. Simpson & W. B. Brockie*, Jan 1937, CHR 45777; Two Thumb Range, *A. P. Druce*, Mar 1985, CHR 401948; Flock Hill, Upper Waimakariri, *L. A. McCaskill*, CHR 141542; OTAGO: Mt Ida, *E. M. Rivers*, 1 Apr 1970, CHR 202554; Lake Benmore, *G. I. Collett*, 4 May 1969, CHR 201894.

ETYMOLOGY: The epithet *nana* refers to the dwarf growth habit of this species.

ILLUSTRATION: Eagle (1982, fig. 93, 94).

CONSERVATION STATUS: Not threatened.

DISCUSSION: *Carmichaelia nana* was accepted by Hooker (1864), Kirk (1899), and Cheeseman (1925), but was abandoned as "*nomen confusum*" by Simpson (1945) and treated as *incertae sedis* by Allan (1961). Simpson (1945) regarded Hooker's (1864) description as comprising "two widely differing plants later described by Colenso as *C. orbiculata* and *C. corrugata*." Simpson however overlooked Hooker's original description and the lectotype in coming to this conclusion. Consequently, *C. nana* is here reinstated. Many early collections identified as *C. nana* often include other dwarf species, as is evidenced by the lectotype sheet at Kew and others at WELT.

13. *Carmichaelia odorata* Benth., in J. D. Hooker, *Fl. nov.-zel.* 1, 50 (1852)

= *C. angustata* Kirk, *Stud. fl. New Zealand*, 114 (1899).

= *C. angustata* var. *pubescens* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand*

75, 243 (1945).

= *C. glabrata* G.Simpson, *Trans. Roy. Soc. N.Z. 75*, 243-244 (1945).

= *C. grandiflora* var. *divaricata* Kirk, *Stud. fl. New Zealand*, 111 (1899) ≡ *C. divaricata* (Kirk) Cockayne, New Zealand plants and their story, ed. 3, 163 (1927).

= *C. pilosa* Benth., in J. D. Hooker, *Fl. nov.-zel.* 1, 50-51 (1852) ≡ *C. odorata* var. *pilosa* (Benth.) Kirk, *Stud. fl. New Zealand*, 113 (1899).

DESCRIPTION (Fig. 3.5): Shrub, up to 3(–8) × 2–3 m. Branches up to 100 mm diameter, ascending and horizontal. Cladodes 40–250 × 1–2.3 mm, erect and spreading, often divaricate, linear, striate, compressed, green, frequently hairy when young, glabrous when mature, apex subacute; leaf nodes 5–14(–19) mm. Leaves 1–7–foliolate, present on seedlings and adults, terminal leaflet larger; lamina 2–13 × 1–8(–13) mm, obovate to broad-elliptic, rarely orbicular, fleshy, green, adaxial and abaxial surfaces hairy or glabrous, apex emarginate, base cuneate; petiole 5–25 mm long, glabrous or hairy, green; petiolule < 0.3 mm long, glabrous or hairy, light green. Leaves on cladodes reduced to scales, < 0.8 mm long, broad-triangular, glabrous, apex acute. Stipules c. 1 × c. 1 mm, free, triangular, adaxial surface glabrous, abaxial surface hairy, apex subacute, margin hairy. Inflorescence a raceme, 1 per node, each with (4–)8-40 flowers. Peduncle 4–10 mm long, glabrous, green. Bracts < 0.8 mm long, triangular, glabrous, brown, apex acute to subacute, margins hairy. Pedicel c. 1 mm long, glabrous, green. Bracteoles < 0.5 mm long, at top of pedicel or on receptacle, green and sometimes flushed red, glabrous, apex obtuse, margin hairy. Calyx 1.5–2 × 1–1.2 mm, campanulate, green, outer surface glabrous. Calyx lobes 0.2–0.3 mm long, triangular, green and usually flushed red, inner surface hairy, appressed to corolla, apex subacute to obtuse. Standard 3.5–4 × 2.5–3.5 mm, broad-obovate, patent, positioned towards front of keel, keeled, apex emarginate, margins flattened; central part of inner and outer surfaces purple or red-purple, margins white, sometimes purple-veined; claw c. 1 mm long, pale green. Wings 3.5–4 × 0.9–1.1 mm, oblong, similar in length to keel, inner and outer surfaces white, sometimes purple-veined, apex obtuse; auricle 0.2–0.4 mm long, triangular, white, apex obtuse; claw 1.3–1.5 mm long, pale green. Keel 3.5–4 ×

1.4–1.7 mm, apex obtuse; distal area of inner surface purple, proximal area white; outer surface white, flushed purple in distal part and sometimes purple-veined; auricle 0.2–0.4 mm long, triangular, white, apex obtuse; claw 1.3–1.5 mm long, pale green. Stamens 3.5–4 mm long; dorsal filaments connate for c. ⅞ of length, outer stamens free for 0.2–0.5 mm. Pistil 3.7–4.2 mm long, exserted beyond stamens, glabrous; ovules 4-9(–11). Pods 5–9 × 1.5–3 mm, oblong, broad-elliptic or ovate, laterally compressed, erect, light grey or brown, valves dehiscent in distal part; beak 1–2.5 mm long, in a central apical position, stout, pungent-tipped. Seeds 2–3.7 × 1.6–2.4 mm, broad-oblong to broad-elliptic, 1–3 per pod, laterally compressed, surface with 1–3 ridges, testa thin and membranous, light brown or tan. Chromosome number $2n = 32$ (Dawson 1995). FL (Sep–)Dec–Feb, FT Jan–May(–Sep).

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia odorata* occurs in the southern part of the North Island and in western and northern parts of the South Island. It occurs in a variety of habitats, but is usually associated with rivers and streams, where it occurs on low terraces, riverbed flats, and forest margins. It is also an early coloniser of disturbed surfaces such as landslips and glacial moraines, and less frequently it occurs in open clearings in forest.

RECOGNITION (Fig. 3.5): *Carmichaelia odorata* and *C. arborea* are recognised by an erect flowering and fruiting peduncle and rachis, erect pods which are dehiscent in the distal part, and flattened seeds which have a thin testa. *Carmichaelia odorata* is distinguished from *C. arborea* in having a longer peduncle and rachis, more flowers, a smaller flower with the keel 3.5–4 mm long (in *C. odorata* 5–6 mm long), a flower with distinct and obvious red-purple coloration on the standard, and smaller pods.

VARIATION: *Carmichaelia odorata* exhibits variation in ovule number, cladodes, and pod size.

Ovule number: The ovule number is variable and the general pattern is of a north-south cline. Plants from the North Island typically have 4 or 5 ovules, those from Nelson and western Marlborough 5 to 7, and those from Westland and Canterbury 6 to 9.

Cladodes: Cladode shape and branching angle varies throughout the range of the species. In the North Island, and in northern parts of Nelson and Marlborough, the cladodes are predominantly straight and have a narrow branching angle. In Westland and southern parts of Marlborough and Nelson the cladodes are usually curved and have a wider branching angle. Plants from Canterbury exhibit the greatest cladode branching angle, sometimes approaching 90°, and the cladodes are often so strongly curved that the tip is below the branching point.

Pods: Pod shape and size are also variable, plants from the North Island having the pods predominantly small and ovate, and those from the southern part of the range in the South Island larger and mostly oblong, while those from the upper part of the South Island are intermediate in size and shape.

Consideration was given to separating *C. odorata* into two subspecies because of apparent discrete variation in cladode branching angle, pod shape and size, and ovule number. Variation of these characters is considered to be clinal, but the differences are accentuated by the absence of collections from western and central Nelson. Indeed, *C. odorata* may not occur in central Nelson, as it was not recorded on a vegetation survey of Tertiary calcareous vegetation of western Nelson by Druce et al. (1987). This gap in the distribution effectively separates plants of coastal and lowland northern Nelson and Marlborough from those of coastal, lowland, and montane areas of southern Nelson, Westland, and Canterbury. Taxonomic recognition at subspecific rank is not being applied, as the differences in cladode branching angle, pod shape and size, and ovule number are not completely discrete, but show some overlap.

REPRESENTATIVE SPECIMENS: WELLINGTON: Moawhango River, *A. P. Druce*, Jan 1950, CHR 116314; Rangitikei River, *D. Petrie*, Jan 1916, CHR 331740; MARLBOROUGH: Tinline River, *P. Wardle*, 25 Jan 1969, CHR 185643; Wakamarina River, *D. Banks 39/91*, 6 Nov 1991, CHR 474120; NELSON: Aorere River gorge, *A. P. Druce*, Feb 1976, CHR 283099; Buller River, *A. W. Wastney*, AK 102866; Wairoa River, *A. P. Druce*, Jan 1981, CHR 387428; CANTERBURY: Organ Range, *B. H. Macmillan 91/24*, 11 Mar 1991, CHR 472400; Hope River, *G. Simpson*, CHR 45702; WESTLAND: Hokitika gorge, *P. Wardle*, 14 Jan 1976, CHR 280012a; Ngahere, *W. R.*

B. Oliver, 19 Apr 1948, CHR 290198a.

ETYMOLOGY: The epithet *odorata* refers to the fragrant flowers.

ILLUSTRATIONS: Burtt (1937), Eagle (1982, fig. 102 and fig. 79 as *C. angustata*), and Wilson & Galloway (1993, fig. 71b as *C. angustata*).

CONSERVATION STATUS: Not threatened.

14. *Carmichaelia petriei* Kirk, *Stud. fl. New Zealand*, 111 (1899)

= *C. petriei* var. *minor* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 271-272 (1945).

= *C. ramosa* G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 272 (1945).

= *C. virgata* Kirk, *Stud. fl. New Zealand*, 112 (1899).

DESCRIPTION (Fig. 3.5, 3.19): Ascending, spreading, or prostrate shrub, up to 2.5 × 2 m. Branches 10–100 mm diameter, stout, ascending, spreading, or prostrate. Cladodes 30–150 × 1–3.5 mm, erect to spreading, linear, striate, terete, or compressed, green, yellow-green, or bronze-green, stout or slender; apex obtuse or subacute, often pungent-tipped, yellow, yellow-green, or green; leaf nodes 4–11. Leaves 1–3–foliolate, present on seedlings, usually absent on adults, terminal leaflet larger; lamina 2.5–12 × 2–7.5 mm, obovate, fleshy, green, adaxial surface glabrous or hairy, abaxial surface hairy, apex emarginate, base cuneate; petiole 2–13 mm long, glabrous or with few scattered hairs, green; petiolule < 1 mm long, glabrous, light green. Leaves on cladodes reduced to scales, < 0.5 mm long, broad-triangular, hairy on adaxial surface, apex subacute. Stipules c. 0.5 × c. 1 mm, free, triangular, apex subacute, margin hairy, adaxial surface glabrous or with few scattered hairs, abaxial surface with few scattered hairs. Inflorescence a raceme, 1–2(–3) per node, each with (3–)6–9 flowers. Peduncle 3–20 mm long, hairy, green and often flushed red. Bracts < 1 mm long, triangular, glabrous

or sparsely hairy, green or red-green, apex acute to subacute, margin hairy. Pedicel 1.5–2.5 mm long, hairy, pale green. Bracteoles < 0.5 mm long, on receptacle or pedicel, green, hairy, apex subacute, margin hairy. Calyx 2–3 × 1.5–1.8 mm, campanulate, green, outer surface hairy and sometimes flushed red. Calyx lobes < 0.5 mm long, triangular, green and usually flushed red, glabrous or hairy, appressed to corolla, apex acute. Standard 4.5–5 × 5.5–6 mm, broad-obovate, patent, positioned in central part of keel, keeled, apex emarginate, margins incurved; inner surface white with various shades of red-purple, veins red-purple, margin often white; outer surface white, often darkened in central part; claw c. 2 mm long, pale green. Wings 4.5–5 × 1.5–2 mm, oblong, exserted beyond keel, white with distal part red-purple and proximal part pale green, apex obtuse; auricle < 0.5 mm long, triangular, pale green; claw c. 1.5 mm long, pale green. Keel 4.5–5 × 1.5–2 mm; distal part red-purple, proximal part white or pale green; auricle c. 0.5 mm long, triangular, pale green, apex obtuse; claw 1.5–2 mm long, pale green. Stamens 4.5–5 mm long; dorsal filaments connate for c. ¾ of length, outer stamens free for c. 1 mm. Pistil 4.7–5.2 mm long, exserted beyond stamens, glabrous; ovules 6–8; stigma with a fringe of hairs below. Pods 5.5–9.5 × 2.5–4.2 mm, broad-elliptic, oblong, broad-oblong, or obovate, laterally compressed, usually pendulous or rarely spreading, light grey or brown; valves dehiscent along upper suture and distal and proximal parts of lower suture, usually long persistent but sometimes dehiscing completely; beak < 1 mm long, on upper suture or occasionally in a central apical position, stout, pungent-tipped. Seeds 1.8–2.6 × 1.2–2 mm, broad-elliptic, reniform, or oblong, 1–4 per pod, green or green-yellow with black mottling, quickly abscising from funicle. Chromosome number $2n = 32$ (Slade 1953; Dawson 1995). FL Nov–Jan, FT Jan–May.

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia petriei* occurs in Otago, Southland (including Stewart Island), the Mackenzie Basin, and the upper part of the Waitaki River valley in south Canterbury. It grows in coastal, lowland, and montane areas of tussock grassland and scrubland, among rock outcrops, in river gorges, on river terraces, on the margins of forest, and on cliffs.

RECOGNITION (Fig. 3.5): *Carmichaelia petriei* is recognised by pods which droop when mature, pod valves which are usually only partially dehiscent and remain attached to the

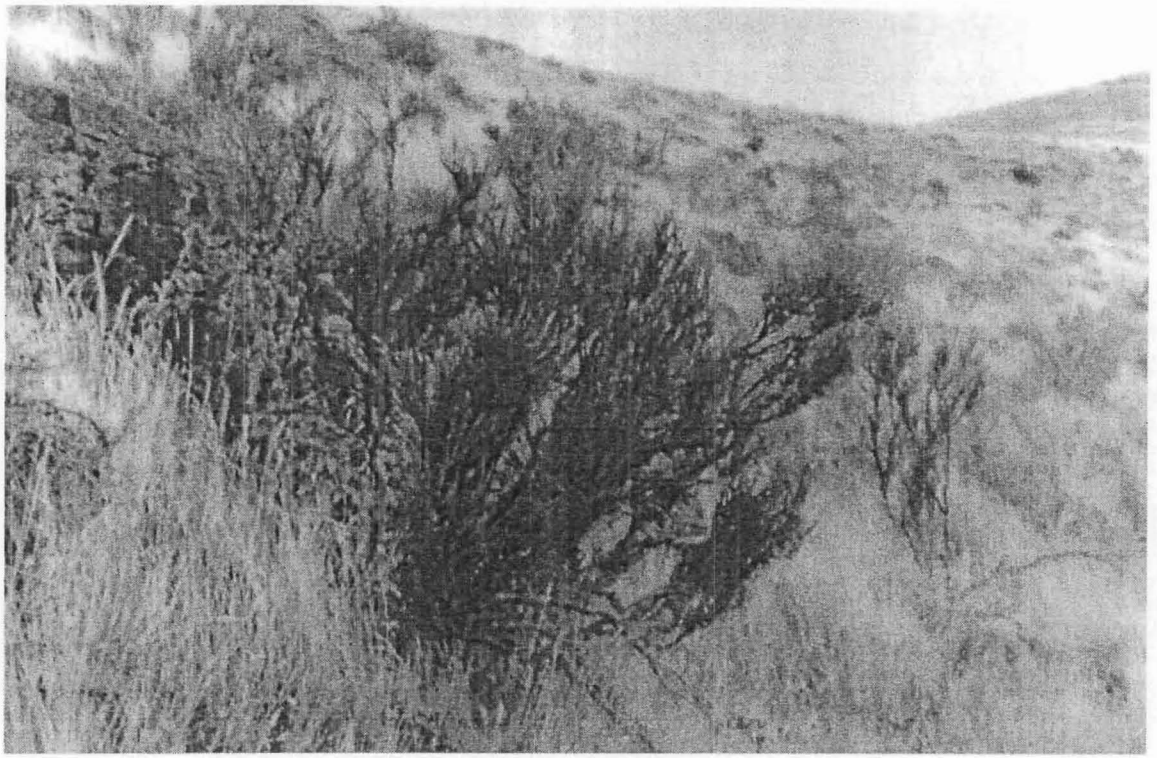


Fig. 3.19 *Carmichaelia petriei*, Waitaki River valley, Otago.

replum, and seeds that abscise from the funicle at maturity. The valves sometimes dehisce completely and then only the replum frame remains. *Carmichaelia petriei* could be confused with *C. australis* but this species has pods with dehiscent valves and seeds which remain attached to the replum.

VARIATION: *Carmichaelia petriei* displays a range of variation in several characters. With the exception of growth habit, which in some forms is phenotypic, the plants have a genetic basis for their variation as the particular features are retained in cultivation.

Pods: Pod size and shape are variable within and between populations, but some general trends are apparent. In the Mackenzie Basin and upper Waitaki River valley the pods are generally large and ovate, in the upper Clutha River, Matukituki River, and Lake Wakatipu areas they are usually smaller and ovate, and in east and south Otago and

Southland they are longer and oblong or broad-oblong.

Cladodes: The cladodes of plants in the semi-arid Mackenzie Basin are yellow or yellow-green, stout, robust, and pungent-tipped; those from Central Otago are yellow-green or green, less stout and robust, and not as pungently tipped; and those from east and south Otago and Southland are green, not stout or robust, and without pungent tips. There is also local variation over relatively short distances. For example, in Little Valley, Central Otago, on dry slopes inhabited by the introduced *Trifolium arvense*, *C. petriei* has yellow-green cladodes with acute yellow tips (NZMS1 S144/290390; CHR 496603). About 19 km away on wet *Chionochloa rubra* tussock grassland *C. petriei* has green cladodes with obtuse or subacute green tips (NZMS1 S144/405235; CHR 496604) (B. P. J. Molloy pers. comm. Apr 1995).

Growth habit: Low, spreading, prostrate, and suckering forms of *C. petriei* occur in the wild alongside shrubby plants. Good examples of this can be seen in the Waitaki River valley and on slopes to the south of Lindis Pass. Several prostrate and rhizomatous plants from south of Lindis Pass have been propagated from cuttings and, when grown on, developed an erect growth form, showing no inclination to develop the prostrate and rhizomatous habit. The reasons for the prostrate growth habit are not understood, and the plants showed no signs of browse damage, which has been observed to induce a similar growth habit in other species. There are also plants intermediate between the typical upright shrubs and the low-growing forms. The prostrate and suckering plants may be a response to harsh environmental conditions, and may have evolved only recently, as they are not yet separable by other morphological characters or ecological preferences. These prostrate forms are regarded as part of the intraspecific variation within *C. petriei*, occurring more regularly in the more continental climate of the Waitaki River valley and Central Otago. A somewhat similar situation occurs with the prostrate *C. appressa* and shrubby *C. australis*, which are sympatric on Kaitorete Spit, Canterbury. However, here *C. appressa* is ecologically separated from *C. australis*.

REPRESENTATIVE SPECIMENS: CANTERBURY: Lake Pukaki, *B. H. Macmillan*, 6 Mar 1970, CHR 211307; Lake Pukaki, *G. Simpson & J. S. Thomson*, Easter 1938, CHR 45781; OTAGO: Lindis Pass, *H. Talbot*, 23 Jan 1965, CHR 301549; Lake Wanaka, *V.*

D. Zotov, 16 Jan 1950, CHR 77080; Kyeburn, *G. Simpson*, Easter 1938, CHR 213074a; Bucklands Crossing, *G. Simpson & J. S. Thomson*, 1937, CHR 45756; Catlins Forest, *E. D. W. Freeman 85/44*, 15 Feb 1985, CHR 417285; Balclutha, *G. Simpson*, CHR 45750; Dansey's Pass, *G. Simpson 474*, 28 Jan 1939, AK 70628; Dunstan Gorge, *D. Petrie*, AK 4865; SOUTHLAND: Makarewa, *G. Simpson*, 4 Feb 1939, CHR 45730; Upukurora Stream, *Simpson & Thomson 306*, CHR 45728.

ETYMOLOGY: The epithet *petriei* commemorates D. Petrie (1846–1925), who first collected this species.

ILLUSTRATIONS: Eagle (1982, fig. 88 and fig. 85 as *C. virgata*), and Wilson & Galloway (1993, fig. 70a).

CONSERVATION STATUS: Not threatened.

15. *Carmichaelia uniflora* Kirk, *Gard. Chron., n.s., 21*, 512 (1884)

= *C. suteri* Colenso, *Trans. & Proc. New Zealand Inst. 23*, 383 (1891) ≡ *C. uniflora* var. *suteri* (Colenso) G.Simpson, *Trans. & Proc. Roy. Soc. New Zealand 75*, 275 (1945).

= *C. uniflora* Buchanan, *Trans. & Proc. New Zealand Inst. 16*, 395 (1884).

DESCRIPTION (Fig. 3.4, 3.20): Dwarf, rhizomatous shrub, up to 20-40(-60) mm × 1 m, forming a dense mat or tufts of cladodes. Rhizomes becoming increasingly stout and woody with age, 50-200 × 1-2.5 mm. Cladodes filiform, linear, striate, compressed, erect to spreading, green to green-yellow, glabrous, 20-40(-60) × 0.75-1.8(-2) mm; apex subacute, yellow to yellow-green; leaf nodes (2-)5-7(-14). Leaves simple, broad-obovate to broad-elliptic, fleshy, entire, green, present on seedlings and absent on mature plants, 5.5-8 × 3-5 mm; adaxial and abaxial surfaces with scattered hairs; apex emarginate to retuse; base cuneate to narrow-obtuse; petiole sparsely hairy, 2-2.5 mm long. Leaves on cladodes reduced to a scale, triangular, glabrous, 0.6-1.5 × 0.8-1.4 mm;

apex acute. Stipules free, triangular, 0.6-1.1 × 0.6-1.2 mm; adaxial surface glabrous; abaxial surface hairy when young, glabrous at maturity; apex acute to sub-acute; margin hairy. Inflorescence a raceme, 1 per node, each with 1(-2) flowers. Peduncle glabrous, occasionally sparsely hairy, green, 4-15 mm long. Bracts, triangular, glabrous, pale green, 0.5-0.8 × 0.5-0.8 mm; apex acute; margin hairy. Pedicel glabrous, occasionally sparsely hairy, pale green, 3-7.5 mm long. Bracteoles at top of pedicel, triangular to narrow-triangular, glabrous, green and occasionally flushed red, 0.2-0.3 × 0.1-0.2 mm; apex acute; margin hairy. Calyx campanulate, c. 2.5 × c. 2.5 mm; inner surface glabrous, green; outer surface glabrous or sparsely hairy, green. Calyx lobes triangular, flushed red, c. 0.5 mm long; apex acute; margin hairy or glabrous. Bud green. Standard obovate, patent, 8-10 × 6-8 mm; adaxial surface white, central area purple, sometimes purple-green veined; abaxial surface green, margin cream-green, sometimes purple-green veined; apex retuse; claw pale green, c. 1.5 mm long. Wings oblong, shorter than keel, 5-6.5 × c. 2 mm; distal area of adaxial surface purple, proximal area green; abaxial surface white, sometimes purple-veined; auricle triangular, pale green, apex obtuse, c. 1.25 mm long; claw pale green. Keel 6-8 × 2.5-3 mm; distal area of adaxial surface purple, proximal area pale green; distal area of abaxial surface dark, proximal area pale green; auricle triangular, pale green, c. 0.75 mm long, with obtuse apex; claw pale green, 2-2.5 mm long. Stamens 7.5-9 mm long; lower filaments connate for c. ⅔ length and outside filaments free for 1.5-2.5 mm. Pistil exserted beyond stamens, c. 10 mm long; style with a ring of hairs below stigma; ovules 9-11. Pod elliptic-oblong, laterally compressed, weakly falcate, black, brown, or grey, one valve dehiscent from base, 7.5-13 × 3-4 mm; beak on adaxial suture, slightly upturned, stout, pungent, 1.5-2 mm long. Seeds oblong-reniform, (2-)4-6(-9) per pod, black, brown, tan, or olive green, 1.2-2 × 1-1.5 mm. Chromosome number $2n = 96$ (Dawson 1989). FL Oct-Mar, FT Nov-May.

DISTRIBUTION AND HABITAT (Fig. 3.24): Nelson, Canterbury, Otago, and Southland. Stable but unconsolidiated river bed gravels, outwash fans, terraces, and stony ground.

RECOGNITION (Fig. 3.4): *C. uniflora* is a dwarf rhizomatous shrub, distinguished from *C. corrugata* by its narrower rhizome; strongly dehiscent pod; cladodes being narrower, less robust, often shorter, and green in colour; and usually single-flowered inflorescence.

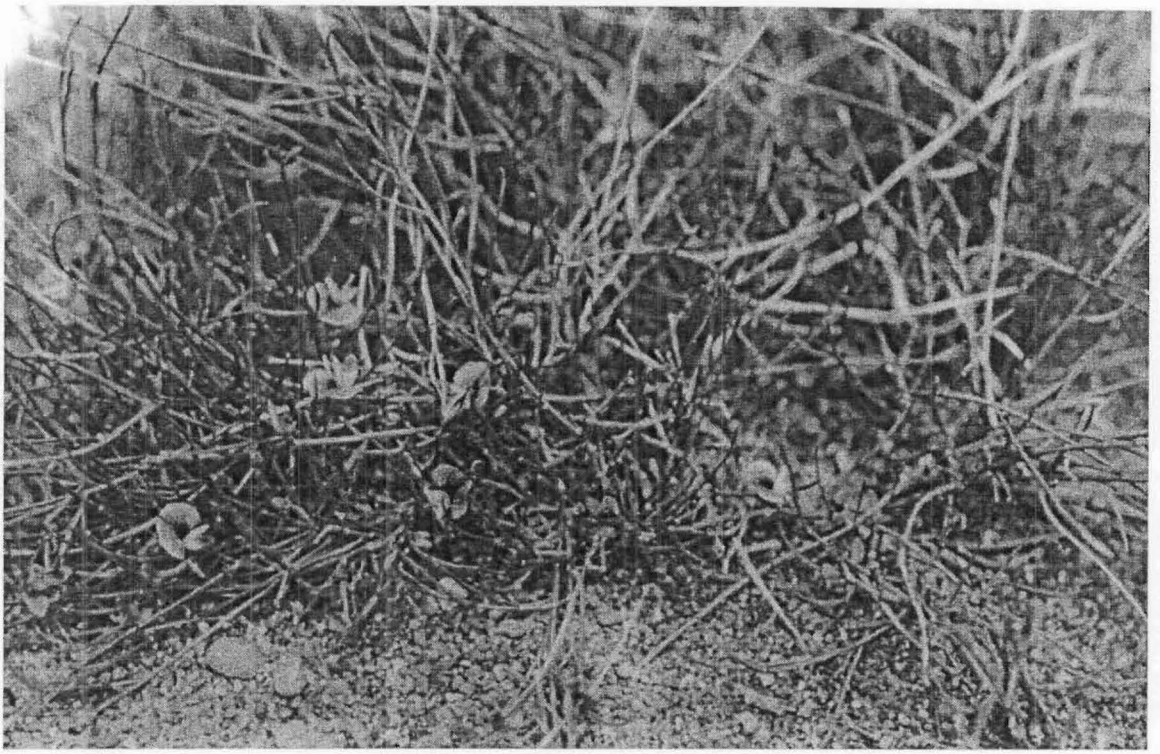


Fig. 3.20 *Carmichaelia uniflora* (cultivated), originally from Greenstone Valley, Otago.

VARIATION: Field study along a 30 kilometre west-to-east stretch of the Waimakarari River between Turkey Flat and the Poulter River suggests a cline in cladode length and width. Plants from Turkey Flat have long and narrow cladodes, whereas plants from terraces at the Poulter River have shorter and wider cladodes. Collections made between the two locations are intermediate between these extremes. The reasons for this variation were not investigated, but may be correlated with mean annual rainfall which decreases eastwards. Plants with narrow and long cladodes would have previously been referred to *C. suteri,* and those with shorter and wider cladodes to *C. uniflora.*

Colour of the standard petal varies from light to dark purple.

REPRESENTATIVE SPECIMENS: NELSON: Matakitaki River, *H. Talbot*, 11 May 1965, CHR 301538; Matakitaki Valley, *W. D. Burke 25*, 17 Nov 1983, CHR 415344;

CANTERBURY: Godley River, *H. D. Wilson*, 23 Feb 1977, CHR 314469B; Bealey River, *B. H. Macmillan 68/290*, 11 Dec 1968, CHR 189644; junction of Waimakariri and Bealey rivers, *P. Wardle*, 22 Dec 1981, CHR 357366; Poulter River, *G. Simpson*, Dec 1936, CHR 215403; Lake Taylor, *H. Talbot*, Dec 1950, CHR 301537; Lake Lyndon, *G. Simpson 96 & J. S. Thomson*, CHR 54264; OTAGO: Matukituki, *J. A. Langbein 14/45*, Dec 1947, CHR 152746; Hunter Valley, *R. Mason 8011*, 28 Dec 1960, CHR 118925; Makarora River, *H. Talbot*, 16 Jan 1953, CHR 185976; SOUTHLAND: Eglinton River, *A. Wall*, Jan 1932, CHR 332003.

ETYMOLOGY: The specific epithet *uniflora* refers to the single flowers which are characteristic of this species.

ILLUSTRATION: Eagle (1982, figs. 97, 98).

CONSERVATION STATUS: Not threatened.

DISCUSSION: *Carmichaelia uniflora* Buchanan was published in May 1884, one month after *C. uniflora* Kirk, and is treated as a later homonym.

16. *Carmichaelia vexillata* Heenan, *New Zealand J. Bot. 33*, 471-474 (1995)

DESCRIPTION (Fig. 3.4, 3.21, 3.22): Dwarf, spreading shrub, up to 0.15 m × 0.4 m. Branches stout, ascending and horizontal, 10-25 mm diameter. Cladodes linear, striate, usually subterete but occasionally compressed, erect to spreading, green and green-yellow, often flushed with red, glabrous or sparsely hairy when young, glabrous at maturity, (20-)40-70(-95) × 1.5-3(-4) mm; apex obtuse, yellow or green, often red in winter; leaf nodes 2-6. Leaves simple, oblanceolate, fleshy, entire, green to green-bronze, present on seedlings and occasionally on mature plants, 4-7.5 × 2-4.5 mm; adaxial and abaxial surfaces with scattered hairs; apex emarginate to retuse; base cuneate; petiole usually glabrous, 1.5-2 mm long. Leaves on cladodes usually reduced to a scale, triangular, glabrous, < 0.5 mm long; apex acute. Stipules free, triangular to narrow-triangular, 0.5-1.1 × 0.6-1 mm; adaxial surface glabrous; abaxial surface

glabrous or with a few sparse hairs, glabrous at maturity; apex acute; margin hairy. Inflorescence a raceme, 1-2 per node, each with 2-3(-5) flowers. Peduncle hairy, green, 3.5-10.5 mm long. Bracts triangular, glabrous, pale green to tan, 0.7-1 × 0.4-0.6 mm; apex acute; margin hairy. Pedicel hairy, pale green, 6-10 mm long. Bracteoles usually absent, if present on pedicel then narrow-triangular, glabrous, 0.2-0.4 mm long; apex acute; margin hairy. Calyx campanulate, 4-5.5 × 2-2.5 mm; inner surface glabrous, green; outer surface glabrous to sparsely hairy, green. Calyx lobes long-triangular to triangular, green, 1-2 mm long; inner surface densely hairy; apex acute; margin hairy. Standard obovate, patent and positioned in central area of keel, keeled, 8-10 × 6.5-7.5 mm; distal and central areas of adaxial surface purple, proximal area pale green, margins white, sometimes purple-veined; distal and central areas of abaxial surface white, proximal area pale green, sometimes purple-veined; apex retuse; margins recurved; claw pale green, c. 3 mm long. Wings oblong, shorter than keel, 7-8 × c. 2 mm; distal and central areas of adaxial surface purple, proximal area green; distal and central areas of abaxial surface white, proximal area pale green; auricle triangular, pale green, apex subacute, c. 1 mm long; claw pale green, c. 2 mm long. Keel 8.5-10 × 3-4 mm; distal and central areas of adaxial surface purple, proximal area pale green; auricle triangular, pale green, c. 1.5 mm long; apex subacute; claw pale green, 3-3.5 mm long. Stamens 8.5-10 mm long; lower filaments connate for c. ⅔ length, and with outside filaments free for 2-3 mm. Pistil similar length to stamens, 8.5-10 mm long; style bearded on adaxial surface; ovary weakly falcate, glabrous; ovules 11-13. Pod oblong to long-elliptic, laterally compressed, weakly falcate, dark brown or light grey, indehiscent or occasionally with one valve partially dehiscent at base, 12-17 × 3-4 mm; beak on adaxial suture, only weakly upturned, stout, pungent, 1-2 mm long. Seeds oblong-reniform, (4-)9-11(-13) per pod, yellow, yellow-green, or olive green, with black mottling, 2-2.75 × 1.5-2.5 mm. FL Nov-Jan, FT Dec-Mar. Chromosome number $2n$ = 32 (M. I. Dawson, pers. comm. May 1994; CHR 471158).

DISTRIBUTION AND HABITAT (Fig. 3.24): Marlborough, South Canterbury, and Otago.

Carmichaelia vexillata joins several other species whose distribution is disjunct between Otago and Marlborough (for discussion see Wardle 1963, Burrows 1965, and McGlone 1985). Recent moraines, alluvium, river terraces, disturbed soils, and soils

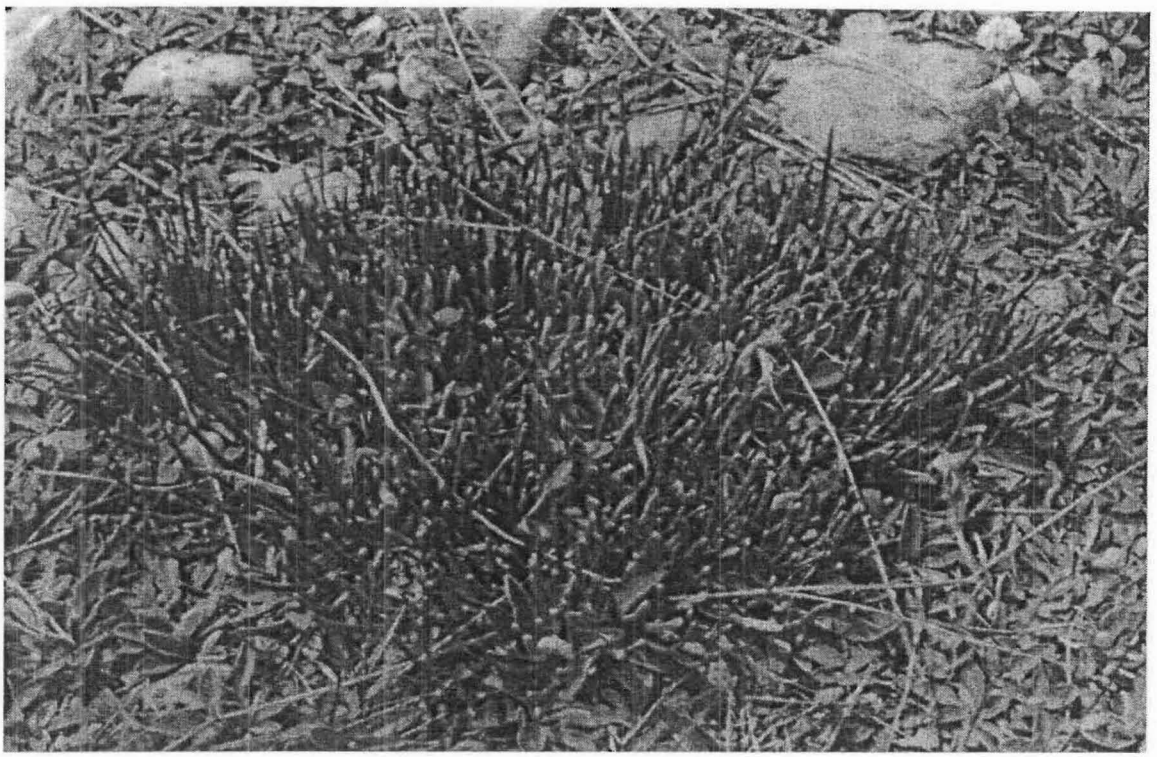


Fig. 3.21 *Carmichaelia vexillata*, near Lake Ohau, Canterbury, the type locality.

derived from schist parent material.

RECOGNITION (Fig. 3.4, 3.22): *Carmichaelia vexillata* is a dwarf shrub similar to *C. astonii* and *C. monroi* but distinguished from both by its subterete (although occasionally compressed) cladodes; having free stipules, even when adnate to the leaf scale; the bracteoles usually absent; the calyx glabrous or only sparsely hairy; and the calyx lobes long, but appressed to the standard and keel petals. It is further distinguished from *C. monroi* by its larger and centrally placed standard, that is longer than the keel, and from *C. astonii* by its smaller habit and flower size.

VARIATION: Plants from Lindis Pass occasionally have broad and flattened cladodes.

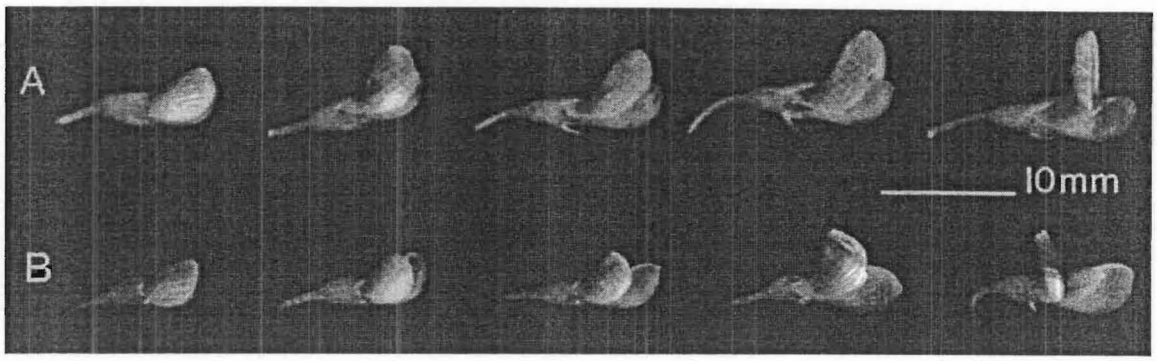


Fig. 3.22 Flower development: **A**, *Carmichaelia vexillata*; **B**, *C. monroi*.

REPRESENTATIVE SPECIMENS: MARLBOROUGH Awatere Valley at Dumgree, *A. W. Wastrey*, CHR 54249; CANTERBURY: Two Thumb Ra., *A. P. Druce*, Mar 1985, CHR 401950; Lake Pukaki, *B. H. MacMillan*, 6 Mar 1970, CHR 207398; Mt John Station, *P. N. Johnson*, 27 Nov 1977, CHR 320147; OTAGO: Waitaki Dam, *G. Simpson*, CHR 54252 Mount Difficulty, *I. Southey*, 11 Mar 1986, CHR 421196; Lindis Pass, *G. Simpson*, CHR 54250A; Mt St Mary, *G. Simpson*, Dec 1938, CHR 54245; Naseby, *D. Petrie*, 23 Dec 1910, CHR 11819; Wether Range, *H. E. Connor*, 21 Jan 1960, CHR 122043; Otematata Station, *G. Simpson*, Dec 1939, CHR 213058; Mt Ida, *Simpson & Thomson 86*, CHR 54248.

ETYMOLOGY: The specific epithet *vexillata* alludes to the standard, which is a diagnostic feature of this species; it is longer than the keel, and also longer than that of the closely related *C. monroi*.

CONSERVATION STATUS: Not threatened.

DISCUSSION: Cockayne (1917) discussed variation in *C. monroi* sens. lat., and suggested that plants from Otago with glabrous calyces "should at least be separated from its allies as a variety." The Cockayne herbarium contains a specimen collected by Petrie from North Otago Botanical District labelled "Carmichaelia humilis", which is an unpublished name.

Simpson too was aware of variation in the *C. monroi* complex. As he resided in Dunedin, it appears that he regarded the local Otago plants with glabrous calyces and the keel and standard of equal length as being typical of *C. monroi.* For plants with hairy calyces and the standard significantly shorter than the keel he provided the name *C. monroi* var. *longecarinata.* Unfortunately Simpson did not examine Hooker's type for *C. monroi*, which has hairy calyces and the standard significantly shorter than the keel. The result of this oversight is that he left the Otago plants unnamed, and *C. monroi* var. *longecarinata* is a heterotypic synonym of *C. monroi.*

17. *Carmichaelia williamsii* Kirk, *Trans. & Proc. New Zealand Inst. 12*, 394 (1880)

DESCRIPTION (Fig. 3.5): Upright and spreading shrub, up to 2–4 × 2–4 m. Branches 50-100 mm diameter, stout, ascending or spreading. Cladodes (130-)180-380 × (5-)8-12 mm, linear, striate, compressed, yellow-green or green, glabrous, apex obtuse; leaf nodes 7-16. Leaves 1-3-foliolate, present on seedlings and rarely on adult plants, terminal leaflet larger; lamina 6-23 × 5-15 mm, elliptic, obovate to broad-elliptic, fleshy, green with yellow marking on proximal part, terminal leaflet larger than lateral leaflets, adaxial surface glabrous, abaxial surface with scattered hairs, apex retuse, base cuneate; petiole 5-15 mm long, with scattered hairs; petiolule 1-5 mm long, with scattered hairs. Leaves on cladodes reduced to scales, < 1 mm long, broad-triangular, abaxial surface with scattered hairs and becoming glabrous with age, apex subacute. Stipules c. 1.5 × c. 1 mm, free, broad-triangular, sometimes with a second pair of smaller denticles, adaxial surface glabrous, abaxial surface with scattered hairs, apex subacute, margin with scattered hairs. Inflorescence a raceme, often in fascicles of 3 or 4 per node, each with (1-)2-4(-5) flowers. Peduncle 1-6 mm long, hairy, green. Bracts 1-1.4 × 0.8-1.5 mm, narrow-triangular to broad-triangular, abaxial surface and margin hairy and becoming sparsely hairy or glabrous with age, apex subacute to obtuse. Pedicel 4-8 mm long, hairy, pale green. Bracteoles 0.4-0.6 × c. 0.2 mm, narrow-triangular to linear, on pedicel, abaxial surface glabrous, or hairy and becoming glabrous with age, apex subacute, margin hairy. Calyx 8-9 × 4.7-5.5 mm, campanulate, green, outer surface glabrous. Calyx lobes triangular, green and usually flushed red, inner surface and margin hairy, appressed to corolla, apex acute. Bud green, becoming

yellow-green at maturity. Standard 18-22 × 11-13.5 mm, ovate, patent, keeled, margins incurved, positioned in proximal part of keel, apex subacute or often weakly retuse, yellow to pale yellow with central part of inner surface and marginal veins maroon-red; claw 8-9 mm long, green. Wings 20-22 × 4-4.5 mm, oblong, falcate, shorter than keel, yellow to pale yellow, apex subacute, margin with a few scattered hairs; auricle 3.5-4.5 × 1.5-2 mm, oblong, pale yellow; claw 5.5-6 mm long, pale green. Keel 25-27 × 7-8 mm, apex narrow and acute, yellow, distal part of inner surface maroon-red; auricle c. 1.5 × c. 1.5 mm, triangular, yellow-green, apex rounded; claw 9-10 mm long, pale green. Stamens 28-30 mm long; dorsal filaments connate for c. ¾ of length, outer stamens free for 6-11 mm. Pistil c. 32-33 mm long, exserted beyond stamens, glabrous except for a small tuft of hairs on inner surface below stigma; ovules (12-)14-16(-17). Pods 23-34 × 6-12 mm, oblong to oblanceolate, laterally compressed, spreading, light to dark brown, valves dehiscent; beak 2-4 mm long, in central apical position, stout, pungent-tipped. Seeds 3-5 × 2-3 mm, reniform to oblong-reniform, (5-)8-15 per pod, dull red to orange-red and sometimes with black mottling, often remaining attached to funicle. Chromosome number $2n = 32$ (Slade 1953). FL May-Nov, FT Oct-May.

DISTRIBUTION AND HABITATS (Fig. 3.23): *Carmichaelia williamsii* is restricted to the Bay of Plenty coast and islands in the Hauraki Gulf in the North Island. In the Aldermen Islands *C. williamsii* occurs on Ruamahua-iti, Hongiora, and Middle Island (Cochrane 1962). On Ruamahua-iti Island it is particularly common in coastal forest and among scrub (Cochrane 1962). *Carmichaelia williamsii* has been described by Oliver (1925) as plentiful on the Poor Knights Islands. In the Hen and Chickens Islands Atkinson (1972) recorded a single plant of *C. williamsii* on Sail Rock, and he also reported a small group near the summit of Araara, an island stack adjacent to Mauitaha.

RECOGNITION (Fig. 3.5): *Carmichaelia williamsii* is readily distinguished from all other species of *Carmichaelia* by its large yellow flowers, large and robust pod, and wide and flattened cladodes. In northern parts of the North Island some populations of *C. australis* also have wide cladodes, and these could perhaps be confused with *C. williamsii*.

VARIATION: The corolla standard varies a little in the size and shade of the red-purple

blotch and the amount of red-purple venation. The growth habit varies with habitat on the Aldermen islands. In coastal forest *C. williamsii* grows as a tall shrub often as high as low shrubby trees, but among windswept coastal scrub it forms compact bushes, and in meadow communities it is semi-prostrate (Cochrane 1962).

REPRESENTATIVE SPECIMENS: SOUTH AUCKLAND: Hick's Bay, *T. Kirk*, CHR 111582; Hick's Bay, *Bishop Williams*, AK 4841; Aldermen Islands, *B. Sladden*, CHR 332023; East Cape, *Bishop Williams*, AK 4824.

ETYMOLOGY: The epithet *williamsii* commemorates W. L. Williams (1827–1926), bishop of Waiapu, who made the first collections of this species.

ILLUSTRATIONS: Summerhayes (1949) and Eagle (1975, fig. 103).

CONSERVATION STATUS: *Carmichaelia williamsii* occurs within a restricted geographical area, has a specific habitat, and apart from large populations on the Poor Knights Islands and the Aldermen islands is usually only sparsely represented at a given locality. In the past *C. williamsii* has been more common along the Bay of Plenty coast, but the few recent collections suggest that it is now restricted to only one or two populations. The classification of vulnerable by Cameron et al. (1995) is supported.

DISCUSSION: Little is known of flowering times in the wild. Plants in cultivation at the Christchurch Botanic Gardens flower regularly during late May and June and again during late October and November. Flowers produced in early winter usually fail to set seed as they are damaged by wind, rain, and low temperatures. Pod development and seed set at the spring flowering is significantly greater. Isolated plants at the Christchurch Botanical Gardens set seed, which suggests that the species is self-compatible. Lloyd (1985) suggested that *C. williamsii* is possibly bird-pollinated, but evidence of this is yet to be provided.

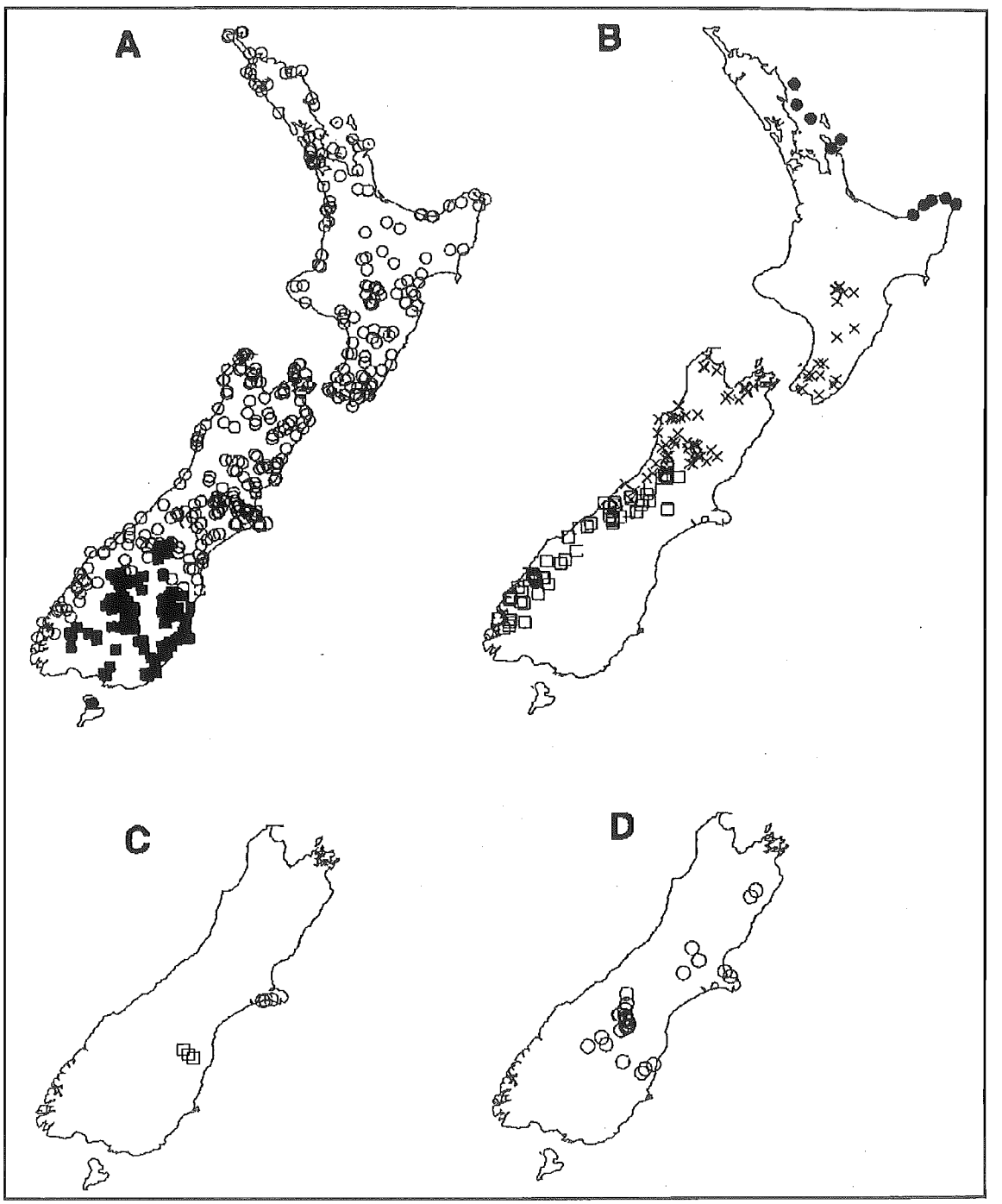


Fig. 3.23 Distributions. **A**, ○ *Carmichaelia australis*; ■ *C. petriei*. **B**, □ *C. arborea*; × *C. odorata*; ● *C. williamsii*. **C**, ○ *C. appressa*; □ *C. hollowayi*. **D**, ○ *C. kirkii*.

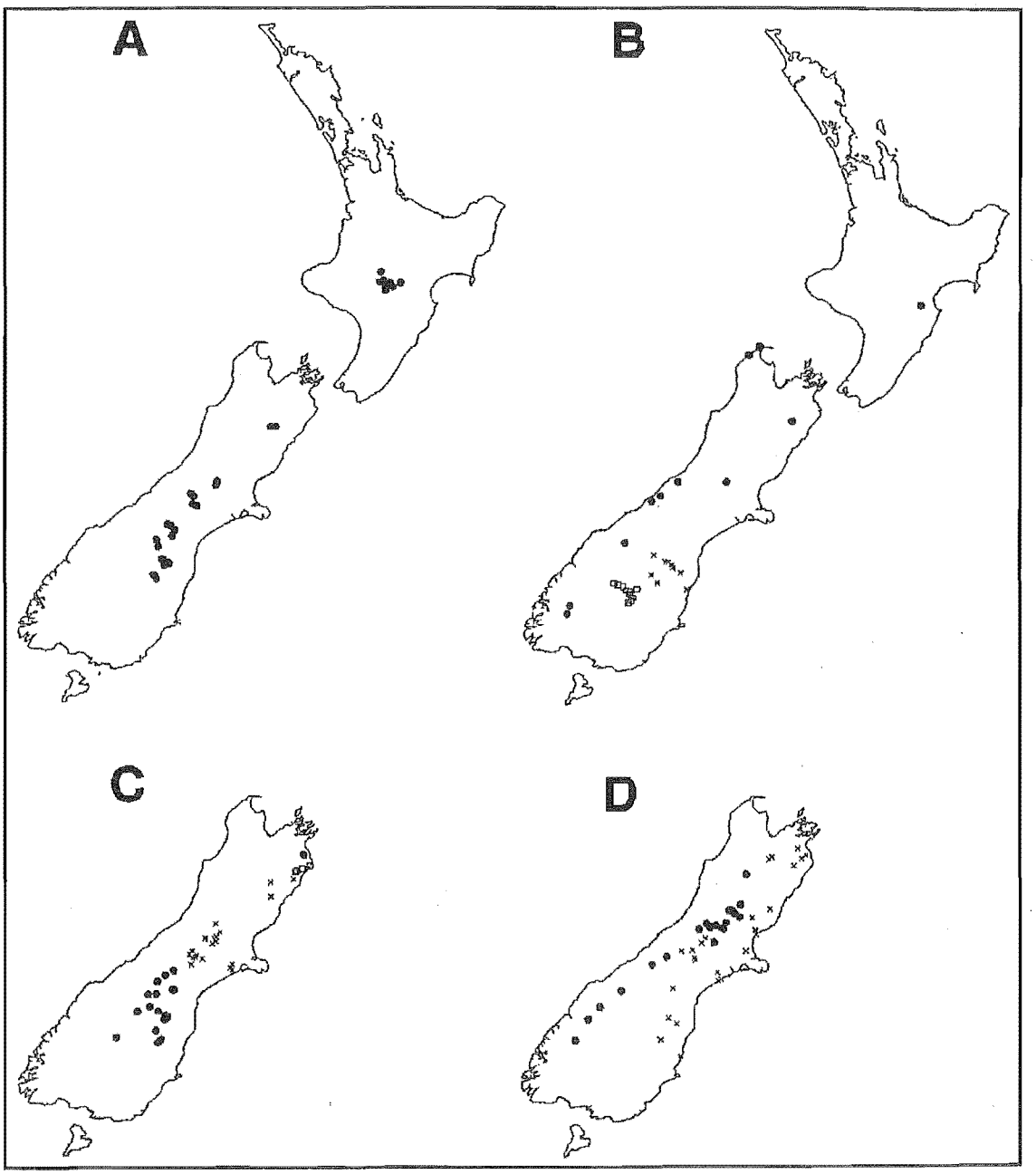


Fig. 3.24 Distributions. **A**, *Carmichaelia nana*. **B**, ▫ *C. compacta*; × *C. curta*; • *C. juncea*. **C**, ▫ *C. astonii*; × *C. monroi*; • *C. vexillata*. **D**, × *C. corrugata*; • *C. uniflora*.

3.6 *NOTOSPARTIUM* REVISION

3.6.1 Introduction

The endemic New Zealand genus *Notospartium* Hook.f. is usually accepted as including three species, *N. carmichaeliae* Hook.f., *N. glabrescens* Petrie, and *N. torulosum* Kirk (Petrie 1921; Cheeseman 1925; Allan 1961; Given 1981; Metcalf 1987; Poole & Adams 1990). However, in recent years the taxonomic status of the two Marlborough endemics, *N. carmichaeliae* and *N. glabrescens* has become confused. Eagle (1982: 276), Wardle (1991: 656), and Smith-Dodsworth (1991) are not clear on what species occur in Marlborough, Druce (1992) and Wilson & Galloway (1993) accept only *N. carmichaeliae*, and other authors have confused the names (Cheeseman 1914; Salmon (1980).

Before *N. glabrescens* was described, Cockayne (1918) reported that Petrie regarded plants from the Clarence Valley as distinct: "Mr. D. Petrie, M.A., suggested to me some time ago that the Clarence Valley plant discovered by Mr. Aston was possibly neither the above [*N. torulosum*] nor *Notospartium carmichaeliae*; and he may quite well be right, as its much-swollen pod looks very distinct." Petrie was very cautious and gave considerable thought to the taxonomy of *Notospartium* prior to the action of describing *N. glabrescens*. Petrie (1921), correctly, made the following observations:

> "I put off describing this species for several years, as I was long uncertain whether it might not prove to be a form of one of the species already described ... In my view the genus contains at least three well-marked species, the habitats which nowhere seem to overlap — *N. carmichaeliae* Hk. f., *N. torulosum* T. Kirk, and *N. glabrescens* ... The flowers of these species are all very much alike in size and form, and one has to fall back on the pods for characters that can be depended on in distinguishing the species ... *N. glabrescens*, is more distinct from the two others than these are one from another ... the pods are not torulose and are much stouter than those of the allied species."

To emphasise the differences in pod shape and size, Petrie (1921) illustrated the pods of all three species of *Notospartium.*

Study of plants in the field, herbarium, and experimental gardens provides further support for Petrie's (1921) acceptance of three species of *Notospartium* and, in particular, that *N. carmichaeliae* and *N. glabrescens* are distinct. Special emphasis is given here to the distribution of these two species, the soils they grow in, and the parent

materials of the soils.

3.6.2 Recognition

Notospartium carmichaeliae, *N. glabrescens*, and *N. torulosum* are alike in being leafless shrubs or small trees up to 8 m, or sometimes 10 m, in height and having a single trunk or several main stems (Fig. 3.25). The flowers of *N. carmichaeliae* and *N. glabrescens* are similar in size and shape, are various shades of pink, are placed on a many-flowered raceme, and are of little use for identification purposes as they are difficult to discriminate. The flowers of *N. torulosum* are also on a many-flowered raceme, but differ from *N. carmichaeliae* and *N. glabrescens* flowers in being lavender and smaller. *N. torulosum* is further distinguished by its slender, green, erect, and more-or-less terete cladodes, and smaller seeds. The fruit is the most reliable feature for identification of all three species. Authors who accept both *N. carmichaeliae* and *N. glabrescens* usually emphasise that the main, and often only difference is pod shape: e.g., "*Notospartium glabrescens* ... is most easily distinguished in the fruiting condition when its larger and fatter pods make confusion impossible" (Burtt 1938); and, *Notospartium glabrescens* "differs from *N. carmichaeliae* only in the size and nature of pods" (Poole & Adams 1990). The fruit of *N. torulosum*, in comparison with the other two species, is more slender, has a thinner valve wall, and is strongly constricted between the seeds — hence the specific epithet *torulosum*.

The key diagnostic features for the two Marlborough species of *Notospartium* are as follows. *N. carmichaeliae* is recognised by: new season's and older cladodes green or light green; bark brown, moderately furrowed, with a rough, usually distinctly lenticellate surface; pods moderately torulose, sparsely hairy on the inner surface; seed outlines visible through the thin valve wall on herbarium specimens with immature and developing pods (Fig. 3.26); green and developing pod valves not fleshy; peduncle, pedicel, and calyx sparsely or moderately hairy; and lower filaments usually persistent on mature fruits.

Notospartium glabrescens is recognised by: new season's cladodes being grey-green, older cladodes grey-green or dark green; bark grey or brown-grey, weakly furrowed, with a more-or-less smooth, indistinctly lenticellate surface; pods not torulose but entire, densely hairy on the inner surface; seed outlines not visible through the thick valve wall on herbarium specimens with immature and developing pods (Fig. 3.26);

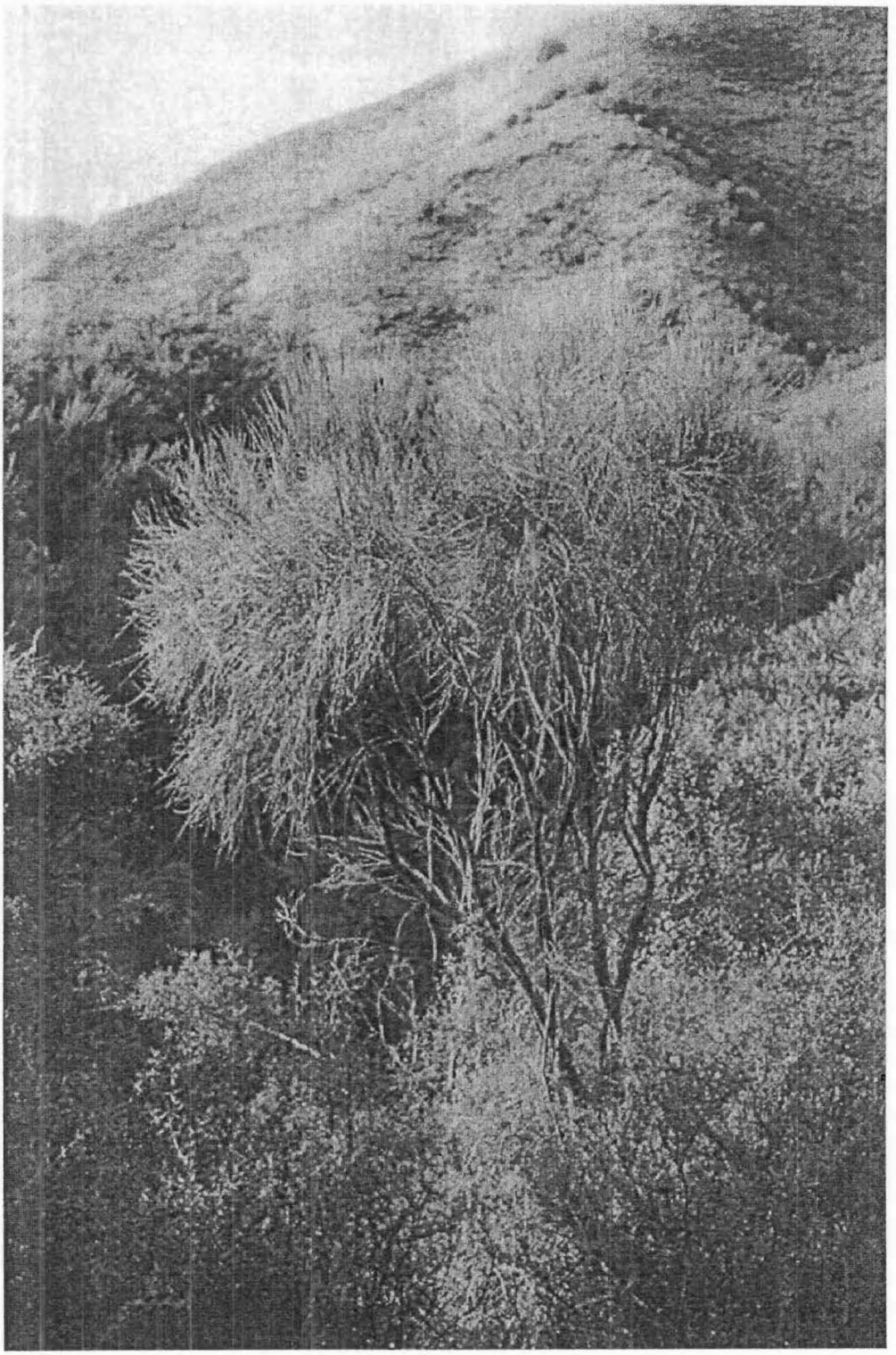


Fig. 3.25 Single-trunk adult plant of *N. carmichaeliae* emergent above riparian scrub, Spray River, Marlborough.

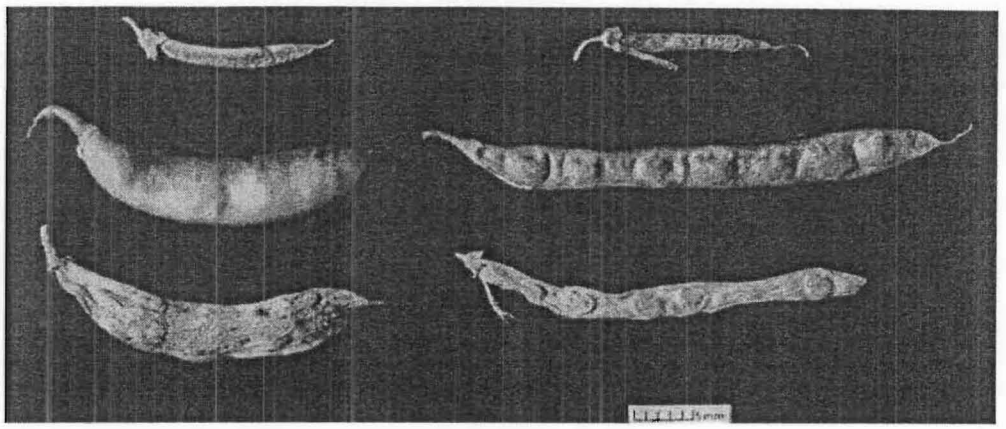


Fig. 3.26 Pods of *N. glabrescens* (left) and *N. carmichaeliae* (right). Top: immature pods from herbarium specimens; middle: mature green and fleshy pods; bottom: mature and dried pods.

green and developing pod valves fleshy; peduncle, pedicel, and calyx glabrous or sparsely hairy; and lower filaments usually absent from mature fruits.

Plants of *N. carmichaeliae* and *N. glabrescens* in cultivation at Lincoln differ in pod colour at maturity but it is not known whether this feature holds for wild plants. The thin pod walls of *N. carmichaeliae* turn brown or grey-brown very quickly once they begin to dry out, whereas those of *N. glabrescens* are thicker, and turn pale yellow-brown or straw-coloured as they dry, becoming brown or grey-brown only after several months.

The common shrubby broom in Marlborough, *Carmichaelia australis* (see Heenan 1996a), when without flowers or fruits, is distinguished from the Marlborough pink brooms by its smaller size, yellow-green cladodes, and the main stems being deeply furrowed and strongly ridged.

REPRESENTATIVE SPECIMENS: ***Notospartium carmichaeliae***: Waihopai Valley, *D. R. Given 11006*, 10 Jan 1978, CHR 482542; Upcot Saddle, *R. V. Mirams*, 4 Mar 1953, CHR 83625; Upcot, *D. Petrie*, Feb 1922, CHR 335342.

Notospartium glabrescens: Isis Stream, *G. Simpson*, Feb 1938, CHR 205068; Woodside Creek, *R. Melville & E. F. Melville*, 7 Jan 1962, CHR 142732; Mead Gorge, *A. P. Druce*, Jan 1976, CHR 279196; near mouth of Clarence River, G. Stevenson, 1914, WELT 26868.

ILLUSTRATIONS: ***Notospartium carmichaeliae***: Hooker (1857, t. 3; 1884, t. 6741), Cheeseman (1914, pl. 36, fig. 1–5), Petrie (1921, fig. 3), Eagle (1975, fig. 101, flowers only; 1978, fig. 30, flowers only), and Salmon (1980, fig. 1, 2, and 9, as *Notospartium glabrescens*).

Notospartium glabrescens: Cheeseman (1914, pl. 36), Petrie (1921, fig. 1), Burtt (1938, t. 9530), Eagle (1975, fig. 101, pods only; 1978, fig. 30, pods only; 1982, fig. 76), Salmon (1980, fig. 3–8), Given (1981, p. 71), and Poole & Adams (1990, p. 113).

3.6.3 Distribution and habitats

Notospartium carmichaeliae and *N. glabrescens* are allopatric and are endemic to the hot dry river valleys of central Marlborough. They are riparian species, inhabiting the sides and crests of bedrock cliffs and bluffs in river gorges, steep, exposed, and partially stable gravel and alluvium, colluvium, and less commonly low river terraces. Plants are generally within 50 m of the river, but sometimes may be up to 200 m above the water level. *Notospartium carmichaeliae* occurs in the western catchments of the middle Awatere and upper Waihopai rivers, including the Grey, Spray, and Avon river valleys and associated tributaries (Fig. 3.27). *Notospartium glabrescens* occurs in the eastern catchments of the Waima, Puhi Puhi, and Kahutara rivers and the tributaries of the middle Awatere and lower Clarence rivers including Jordan River, Medway River, Dee Stream, Mead Stream, and George Stream (Fig. 3.27). *Notospartium torulosum* is a Canterbury endemic, occurring along the foothills of the Southern Alps. Its southern limit is the Tengawai River, but it also occurs at Te Moana Gorge, Lynn Stream, Selwyn River, and Rockwood Range in mid Canterbury, and Whales Back, Limestone Stream, Pettrill Stream, and Mason River in north Canterbury (Fig. 3.27).

The close taxonomic relationship between *N. carmichaeliae* and *N. glabrescens* and the allopatry of all three species of *Notospartium* suggest that there are important factors underlying their distribution. For *N. carmichaeliae* and *N. glabrescens* the Awatere River valley is of particular interest as both species occur in this valley and its

tributaries, but their distributions do not overlap. The Awatere Fault is a significant geological feature of the valley, running parallel with the river on the true left bank from its source on Molesworth Station to its mouth (Lensen 1962). *N. carmichaeliae* occurs along tributaries on the true left of the middle Awatere River near Upcot Saddle and in the Grey River catchment, all to the north-west of the Awatere Fault. On the true right of the Awatere River, *N. glabrescens* is known from the Hodder, Cam, Isis, Jordan, and Medway rivers, all to the south-east of the Awatere Fault. In the southern part of its distribution, *N. glabrescens* is bounded by the Hope Fault, which also marks the northern limit of *N. torulosum* (Fig. 3.27).

These three distinct species with well defined allopatry provide support for the tectonic hypothesis of plant distributions proposed by McGlone (1985). *Notospartium carmichaeliae* has a similar distribution to *Leucogenes neglecta*, which is bounded by the Alpine Fault in the Wairau River valley and the Awatere Fault (Molloy 1995).

The allopatry of *N. carmichaeliae*, *N. glabrescens*, and *N. torulosum* is unlikely to be exclusively attributable to tectonic activity, and other environmental (McGlone 1985) and geological factors may be involved. For instance, the Awatere Fault (Fig. 3.27) separates different lithologic types within the Torlesse Supergroup. To the north-west, where *N. carmichaeliae* occurs (Fig. 3.27), are highly sheared, well indurated, graded-bedded greywacke and argillite of Triassic age, massive greywacke with `cannonball' concretions, and well indurated, graded-bedded greywacke and argillite of Jurassic age; these rocks have complex folding and faulting (Lensen 1962). To the south-east of the fault, where *N. glabrescens* occurs (Fig. 3.27), the basement rocks of the Inland and Seaward Kaikoura ranges are Jurassic graded-bedded greywacke and argillite overlain by massive greywacke with `cannonball' concretions and conglomerate bands, and graded-bedded greywacke in the upper part of the sequence (Lensen 1962). In this region *N. glabrescens* occurs on Amuri limestone, greensand, mudstone, siltstone, and sandstone rocks. Druce & Williams (1989) surveyed the vegetation patterns of the Benmore-Chalk Range area and noted that *N. glabrescens* (treated by Druce & Williams as *N. carmichaeliae*) is more common on cliffs of Tertiary materials than on Cretaceous mudstone. In the Chalk Range, *N. glabrescens* grows on Amuri limestone, but does not occur on adjacent Jurassic greywacke of the Torlesse Supergroup (S. Courtney pers. comm.). Furthermore, neither species crosses the Awatere Fault; to the south-east *N. carmichaeliae* does not grow on soils derived from

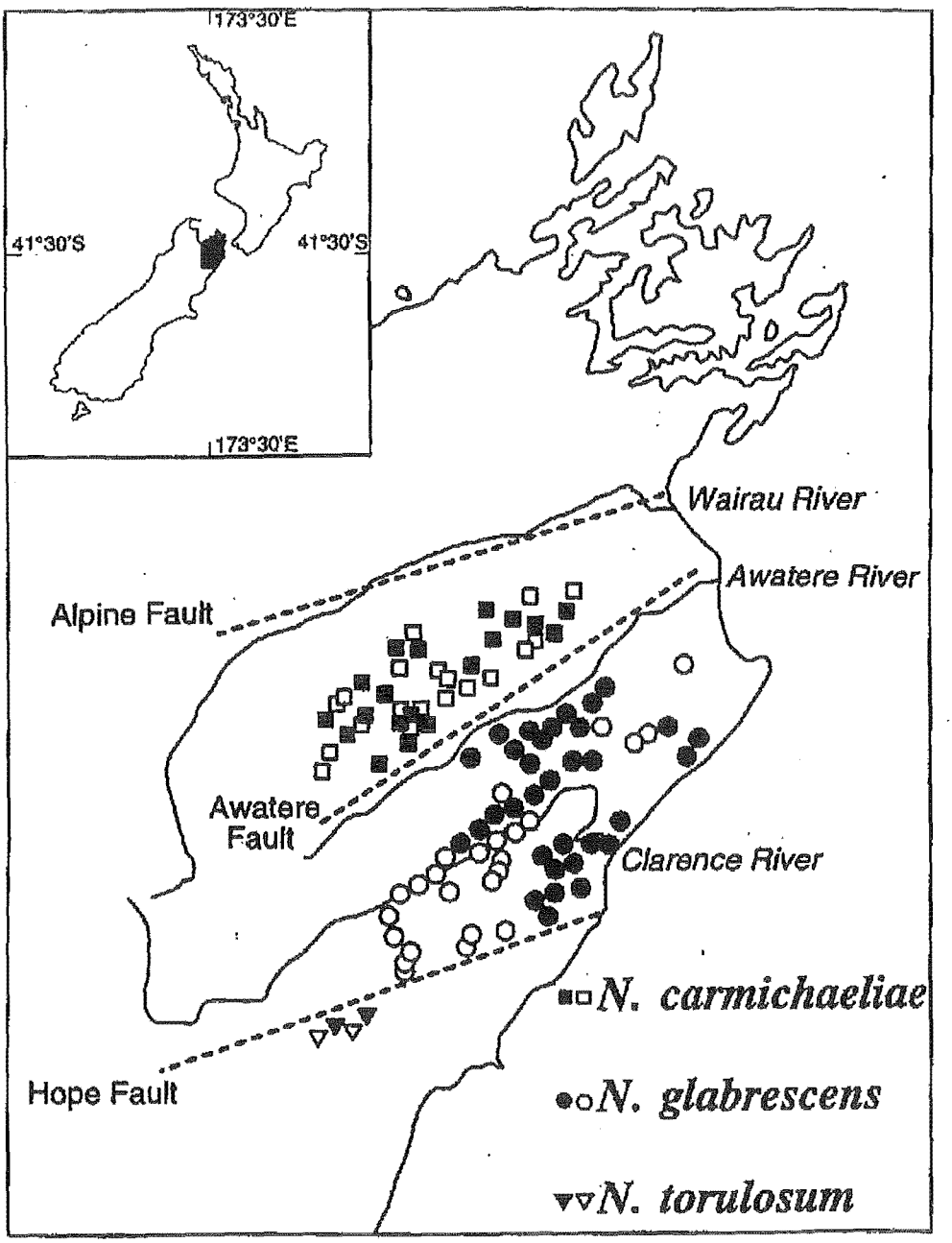


Fig. 3.27 Distribution of *Notospartium carmichaeliae* and *N. glabrescens* in Marlborough, and northern limit of *N. torulosum* in Canterbury. *N. carmichaeliae*: ■ herbarium voucher; □ field record from S. Courtney. *N. glabrescens*: ● herbarium voucher; ○ field record from S. Courtney. *N. torulosum*: ▾ herbarium voucher; ▿ field record from A. W. Purdie and P. B. Heenan.

the Jurassic basement rocks of the Kaikoura Ranges, and to the north-west *N. glabrescens* does not occur on isolated outcrops of base-rich rock.

To assess the relationship between parent materials and the distribution of *N. carmichaeliae* and *N. glabrescens*, rock samples from the habitat of three populations of *N. carmichaeliae* and four of *N. glabrescens* were collected and analysed (Table 3.3). In response to a hydrochloric acid test for calcium carbonate ($CaCO_3$), the parent materials from the habitat of *N. carmichaeliae* gave no reaction, while those of *N. glabrescens* all fizzed indicating the presence of $CaCO_3$. To further determine the influence of parent materials on the distribution of *N. carmichaeliae* and *N. glabrescens*, a semiquantitative element analysis was conducted (for results see Table 3.3). The parent materials from the *N. carmichaeliae* habitats all had low levels of calcium (Ca), magnesium (Mg), potassium (K) and sodium (Na), moderately low levels of aluminium (Al), and high levels of silicon (Si). In comparison, three of the parent materials from *N. glabrescens* habitats had moderate to high levels of Ca, low levels of Mg, K, Na, and Al, and low to moderate levels of Si. The parent material collected from the fourth *N. glabrescens* habitat at the Medway River was most similar to the parent materials of *N. carmichaeliae* in having low levels of Ca, Mg, K, and Na, a moderately low level of Al, and a high level of Si. Although the level of Ca is low in this sample the slight fizz response indicated the presence of $CaCO_3$. Phosphorus is present in very low amounts in all samples. These results indicate that *N. glabrescens* grows on parent materials with calcium carbonate present, whereas *N. carmichaeliae* has no such preference. The Medway River site with its low Ca level is particularly instructive, as this suggests that the level of Ca present in the parent material does not have to be high for *N. glabrescens* to occur.

To establish whether the soils derived from particular parent materials show some correlation with species distributions, soil samples from two populations of *N. carmichaeliae* and three of *N. glabrescens* were collected and analysed by quick-test (Table 3.4). The Woodside Creek and the Clarence soils of *N. glabrescens* are fully base saturated, whereas the Medway soil has a moderately high level of base saturation and is therefore more similar to the Waihopai soils of *N. carmichaeliae*. The percentage of calcium making up the cation exchange capacity (CEC) is very high for the Woodside and Clarence (*N. glabrescens*) soils, and moderate for the Medway (*N. glabrescens*) and Waihopai (*N. carmichaeliae*) soils. The values for the minor

constituents K, Mg, and Na are similar in both sets of soils in being low to very low. Both sets of soils have low values for available phosphorus, and this appears to be closely correlated with the low levels of total phosphorus in the parent materials. It is therefore possible that phosphorus does not play an important role in the soil preferences of these species and, in particular, *N. glabrescens*. However, younger soils are likely to have higher phosphorus levels, and it is on these soils that seedlings of *N. glabrescens* would be likely to establish. There is some variation between the composition of parent materials and soils and this could be due to differing ages of the soil samples, different stages of soil development, including factors such as humus content, and natural depositions of other material such as loess and flood debris.

The most significant difference between the two groups of soils is the pH: the soils on which *N. glabrescens* occurs are moderately alkaline, while those of *N. carmichaeliae* are slightly acidic. Soil pH therefore appears to be a very important factor in the habitat preferences of the two species. The parent material at the Medway River *N. glabrescens* site is instructive as the only significant difference between it and those of *N. carmichaeliae* is the presence of calcium carbonate.

In a study of British calcicoles Steele (1955) concluded that pH and Ca were the two most important factors in their distribution. Steele found that calcicoles vary quantitatively in their pH and Ca requirements, and that high pH can partly compensate for low Ca, and high Ca can partly compensate for low pH. At the *N. glabrescens* Medway site it is likely that a moderately alkaline pH has partly compensated for the low level of calcium in the parent material and therefore the low calcium % of CEC in the soil sample. If the Medway River samples had not been included in the analysis it could have been incorrectly concluded that *N. glabrescens* requires moderate to high levels of Ca when compared to *N. carmichaeliae*.

Molloy (1994) has argued that in New Zealand too narrow a concept of the term calcicole has been used, and that a more appropriate definition would embrace plants showing a preference for all base-rich materials, not just limestone. *Notospartium glabrescens* adequately fits this description, occurring on Cretaceous and Tertiary mudstone, sandstone, and siltstone as well as Amuri limestone.

3.6.4 Conservation status

Notospartium carmichaeliae and *N. glabrescens* occupy a strictly riparian habitat,

and are subject to similar threats. These include aerial spraying for control of introduced gorse and broom (Given 1981), browsing by goats, sheep, and cattle, and competition from naturalised species. The impact of weedy species is likely to be a problem for only a small number of populations, as plants usually occur on steep, exposed, and generally inaccessible bluffs.

These species are in relative terms very successful inhabitants of the riparian zone in central Marlborough. Their perception as rare plants being partly a result of limited distributions based on specific habitat requirements, and in part to our poor understanding of their past and current distribution and abundance. They appear to have no reproductive constraints, as both species regularly produce large numbers of flowers and reasonable amounts of seed. Germination rates in the wild are not known, but seed readily germinates in the nursery situation. *N. carmichaeliae*, *N. glabrescens*, and *N. torulosum* are at least capable of self-pollination and self-fertilisation, as isolated cultivated plants produce viable seed.

Notospartium carmichaeliae was perhaps once more widely distributed. Kirk (1896) recorded that *N. carmichaeliae* "unhappily has been extirpated in many habitats", and a short time later he added that it "has now become extremely rare" (Kirk 1899). Recently, Given (1981) listed *N. carmichaeliae* as vulnerable and *N. glabrescens* as local, while Cameron et al. (1993) regarded *N. carmichaeliae* as local and *N. glabrescens* as insufficiently known. The latest threatened plant list (Cameron et al. 1995) gives *N. carmichaeliae* as local, while *N. glabrescens* has been removed from the list as it is now known to be more common than previously thought. *N. glabrescens* is known from several large populations with hundreds of individuals of various height and age classes, and I endorse its removal from the threatened plant list. *N. carmichaeliae* occurs over a slightly smaller area than *N. glabrescens* and is known from only two populations which number in the hundreds. It should be regarded as a local plant which needs to be regularly monitored, since if either population were subjected to habitat disturbance or destruction, it could easily become either endangered or vulnerable.

Table 3.3 Analysis of parent materials at selected sites of *Notospartium carmichaeliae* and *N. glabrescens*.

	N. carmichaeliae (between the Wairau and Awatere Faults)			*N. glabrescens* (between the Awatere and Hope Faults)			
Location	Spray Point, Waihopai R.	Sweet Stream, Waihopai R.	Avon River	Isis Stream, Awatere R.	Clarence River	Woodside Creek	Medway River
(NZMS 260)	O29 488417	O29 560493	O29 623472	O29 678276	P30 825961	P30 989192	P29 823344
Parent material	well indurated, fine-grained Torlesse mudstone	well indurated, fine-grained Torlesse sandstone	well indurated, medium- to coarse-grained Torlesse sandstone	well indurated, fine-grained Torlesse calcareous mudstone	well indurated, fine-grained limestone with calcite veins	well indurated, fine-grained silacaceous limestone	weakly indurated, fine-grained mudstone
HCl effervescence	no reaction	no reaction	no reaction	strong fizz	strong fizz	strong fizz	slight fizz
Calcium (%)	1.32	1.02	1.22	22.95	45.39	30.02	1.52
Magnesium (%)	1.79	1.54	1.27	0.94	0.20	0.35	1.92
Potassium (%)	1.50	3.18	1.91	1.43	0.06	0.26	3.32
Sodium (%)	2.23	1.52	2.66	1.14	0.05	0.11	1.47
Aluminium (%)	7.23	8.90	7.75	4.79	0.40	0.94	8.98
Silicon (%)	37.17	35.22	36.01	20.93	6.11	20.70	34.50
Phosphorus (%)	0.11	0.12	0.09	0.09	0.04	0.04	0.11

Table 3.4 Chemical analysis of soils for *Notospartium carmichaeliae* and *N. glabrescens* from selected sites. Location details as in Table 3.3.

	N. carmichaeliae		*N. glabrescens*		
Location	Spray Point, Waihopai River	Sweet Stream, Waihopai River	Clarence River	Woodside Creek	Medway River
pH	6.1	6.5	8.1	7.8	7.8
Olsen P ppm	12	7	1	1	4
CEC (pH7) me./100 g	16.78	25.88	39.78	17.18	11.33
Base saturation %	81.6	97.4	(100)	(100)	93.5
Calcium % of CEC	63.4	72.2	98.5	98.9	69.7
Exch. Ca me./100 g	10.7	18.7	39.2	17.0	7.9
Exch. Mg me./100 g	2.38	5.23	2.43	0.76	1.58
Exch. K me./100 g	0.49	1.17	0.47	0.5	1
Exch. Na me./100 g	0.16	0.13	0.42	0.18	0.11

3.7 KEY TO THE INDIGENOUS SPECIES OF *CARMICHAELIA*, *CHORDOSPARTIUM*, *CORALLOSPARTIUM*, AND *NOTOSPARTIUM*

Many species of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* are difficult to distinguish and identify, and frequently only flowering material or fruiting material is available. For these reasons the key presented here is designed to contend with vegetative, floral, and fruit characters together, or fruit and floral by themselves. Thus, near the start of the key three choices are provided that depend on the availability of plant material. A limitation of only having flowering or fruiting material available is that it is often difficult to key out plant material to a single species, and frequently several choices will be given. Pod characters are taken from fully mature pods.

1	Material with either flowers or fruit, but not both	*2*
1	Material with both flowers and fruit	*3*
2	Material with flowers only	*29*
2	Material with fruit only	*42*
3	Flowers yellow, keel > 15 mm long; cladodes > 12 mm wide	***C. williamsii***
3	Flowers pink, purple, lavender, or violet, keel < 12 mm long; cladodes < 8 mm wide	*4*
4	Liane, not rhizomatous; seeds mottled blue/black and white; pith round	***C. kirkii***
4	Shrub or subshrub, sometimes rhizomatous; seeds yellow-green, green, red, often mottled; pith compressed	*5*
5	Pod indehiscent	*6*
5	Pod dehiscent	*19*
6	Ovary and pod hairy; cladodes distinctly grooved	*7*
6	Ovary and pod glabrous; cladodes not obviously grooved	*9*
7	Style glabrous, keel < 5 mm long, wings longer than keel	***Ch. muritai***
7	Style bearded, keel > 5 mm long, wings shorter than keel	*8*
8	Woody shrub to about 2 m; young cladodes on adult plants usually erect but sometimes spreading, cladodes stout, deeply grooved; flowers	

	in fascicles	***Co. crassicaule***
8	Large shrub or small tree; young cladodes on adult plants drooping, cladodes slender, shallowly grooved; flowers in a raceme, often branched	***Ch. stevensonii***
9	Wings shorter than keel, keel > 6 mm long; pod usually > 10 mm long, sometimes constricted	*10*
9	Wings longer than keel, keel < 5 mm long; pod < 8 mm long, not constricted	*17*
10	Large shrubs or small trees; pods sometimes constricted, valves usually flat	*11*
10	Subshrubs, sometimes rhizomatous; pods not constricted, valves inflated	*13*
11	Pods not constricted between seeds; seed outline not visible through dry fruit wall; plant from between the Awatere River and the Hope Fault	***N. glabrescens***
11	Pods constricted between seeds; seed outline often visible through dry fruit wall; plant not occurring between Awatere River and Hope Fault	*12*
12	Flowers pink; seeds usually > 2 mm long; pods weakly constricted; plant from Marlborough between Awatere and Wairau rivers	***N. carmichaeliae***
12	Flowers lavender; seeds usually < 2 mm long; pods strongly constricted; plant from Canterbury	***N. torulosum***
13	Plants not rhizomatous; pods indehiscent; standard usually whitish on abaxial surface	*14*
13	Plants rhizomatous; pods usually dehiscent at base, but sometimes indehiscent; petal usually greenish on abaxial surface	*16*
14	Calyx glabrous; standard positioned near basal part of keel	***C. vexillata***
14	Calyx hairy; standard positioned near central part of keel	*15*
15	Pods up to 23 mm long; calyx weakly hairy and lobes 2-2.5 mm long; restricted to limestone in Marlborough	***C. astonii***
15	Pods up to 15 mm long; calyx densely hairy and lobes < 1mm long; various habitats in Canterbury and Marlborough	***C. monroi***
16	Cladodes green, 0.75-2 mm wide; inflorescences 1(-2)-flowered	***C. uniflora***
16	Cladodes orange-green or yellow-green, 1.5-3.5 mm wide; inflorescences 2-flowered	***C. corrugata***
17	Plants prostrate; pods of uniform width along their length; peduncle	

	< 5 mm long	*C. juncea*
17	Plants erect or spreading; pods distinctly broader at distal end; peduncle > 5 mm long	*18*
18	Sprawling, decumbent, often straggling shrub (although sometimes in compact mounds when grazed); cladodes sparsely placed, olive-green to brown-green, with purplish bloom when young, often brown or bronze in winter; pod 2-2.5 mm wide	*C. curta*
18	Erect and spreading shrub, sometimes decumbent; cladodes crowded, green (rarely brown), and without obvious bloom; pod 3-4 mm wide	*C. compacta*
19	Wings shorter than keel, style bearded	*20*
19	Wings longer than keel, style glabrous	*23*
20	Rhizomatous dwarf shrub	*21*
20	Upright or spreading shrub or climber, not rhizomatous,	*22*
21	Cladodes green, 0.75-2 mm wide; inflorescences 1(-2)-flowered	*C. uniflora*
21	Cladodes orange-green or yellow-green, 1.5-3.5 mm wide; inflorescences 2-flowered	*C. corrugata*
22	Shrub; cladodes > 6 mm wide and compressed; pith compressed; standard 18-22 mm long and yellow with reddish blotch, keel > 15 mm long	*C. williamsii*
22	Liana or shrub; cladodes < 5 mm wide and terete; pith circular; standard 8-9 mm long and white with red-purple blotch, keel < 10 mm long	*C. kirkii*
23	Subshrub; cladodes < 50 mm long	*C. nana*
23	Upright, spreading, or prostrate shrub; cladodes much longer than 50 mm	*24*
24	Inflorescences and pods always ascending, dehiscing at the apex; seeds with a thin testa	*25*
24	Inflorescences and pods ascending, spreading, or drooping, dehiscing along the dorsal or ventral sutures or at base; seeds with a thick testa	*26*
25	Pod 5-9 mm long; (4-)8-40 flowers per inflorescence; keel 3.5-4 mm long, standard white but with a prominent coloured blotch	*C. odorata*
25	Pod 7-15 mm long; 5-10 flowers per inflorescence; keel 4-6 mm long, standard usually white and sometimes with a dark blotch	*C. arborea*
26	Pod valves usually fully dehiscent; seed persistent	*27*
26	Pod valves partially dehiscent; seed deciduous	*28*

27	Prostrate shrub; restricted to Kaitorete Spit, Canterbury	***C. appressa***
27	Upright or spreading shrub; widespread in New Zealand	***C. australis***
28	Sprawling shrub, usually rhizomatous; pod valves compressed; restricted to limestone in the Waitaki River valley	***C. hollowayi***
28	Upright or spreading shrub, rarely rhizomatous (when browsed); pod valves concave; in Otago and Southland	***C. petriei***

FLOWERS

29	Flowers yellow, keel > 15 mm long	***C. williamsii***
29	Flowers pink, purple, lavender, or violet, keel < 12 mm long	*30*
30	Ovary hairy	*31*
30	Ovary glabrous	*33*
31	Style bearded, keel > 5 mm long, wings shorter than keel	*32*
31	Style glabrous, keel < 5 mm long, wings longer than keel	***Ch. muritai***
32	Inflorescence a fascicle	***Co. crassicaule***
32	Inflorescence a raceme, sometimes branched	***Ch. stevensonii***
33	Wings shorter than keel, keel > 6 mm long	*34*
33	Wings longer than keel, keel < 6 mm long	*40*
34	Flowers pink	***N. carmichaeliae***, ***N. glabrescens***
34	Flowers purple, lavender, or violet	*35*
35	Inflorescence a raceme > 3 cm long	***N. torulosum***
35	Inflorescence a raceme < 3 cm long	*36*
36	Standard usually greenish on abaxial surface	***C. corrugata***, ***C. uniflora***
36	Standard usually off-white on abaxial surface	*37*
37	Standard orbicular to broad-obovate	***C. kirkii***
37	Standard obovate	*38*
38	Calyx glabrous; standard positioned in basal part of keel	***C. vexillata***
38	Calyx sparsely to densely hairy; standard positioned in central part of keel	*39*
39	Calyx sparsely hairy, lobes 2-2.5 mm long	***C. astonii***
39	Calyx densely hairy, lobes < 1 mm long	***C. monroi***
40	Inflorescences ascending, spreading, or drooping	***C. appressa***, ***C. australis***, ***C. compacta***, ***C. curta***, ***C. hollowayi***, ***C. juncea***, ***C. nana***, ***C. petriei***
40	Inflorescences ascending	*41*
41	Keel 3.5-4 mm long, standard with a prominent coloured blotch	***C. odorata***

41	Keel 4-6 mm long, standard with a dark blotch	***C. arborea***

FRUIT

42	Pod indehiscent	*43*
42	Pod dehiscent	*51*
43	Pod hairy	*44*
43	Pod glabrous	*46*
44	Pod c. 3.5 × c. 1.8 mm	***Ch. muritai***
44	Pod c. 6 × 3-4 mm	*45*
45	Inflorescence a fascicle	***Co. crassicaule***
45	Inflorescence a raceme, sometimes branched	***Ch. stevensonii***
46	Pod < 7 mm long, dorsiventrally compressed	*47*
46	Pod > 7.5 mm long, laterally compressed	*48*
47	Pod oblong to slightly linear in top view	***C. juncea***
47	Pod obovate in top view	***C. compacta*, *C. curta***
48	Pod falcate, drying black, grey, or dark-brown, never torulose	***C. astonii*, *C. corrugata*, *C. monroi*, *C. uniflora*, *C. vexillata***
48	Pod linear to linear-oblong, drying light-brown or straw coloured, sometimes torulose	*49*
49	Pod not torulose, seeds in two rows	***N. glabrescens***
49	Pod torulose, seeds in one row	*50*
50	Pod strongly torulose, frequently twisted or contorted	***N. torulosum***
50	Pod weakly torulose, never twisted or contorted	***N. carmichaeliae***
51	Inflorescences ascending; pods dehiscent at apex; seeds with a thin testa	*52*
51	Inflorescences ascending, spreading, or drooping; pods dehiscent at base or on lateral walls; seeds with a thick testa	*53*
52	Inflorescences with 5-10 pods; pods 7-15 mm long	***C. arborea***
52	Inflorescences with (4-)8-40 pods; pods 5-9 mm long	***C. odorata***
53	Pods with a large prominent central apical beak; seeds mottled blue/black and white	***C. kirkii***
53	Pods with a small apical beak; seeds yellow-green, green, red, often mottled these colours	*54*
54	Pod valves slightly dehiscent at base	***C. astonii*, *C. corrugata*, *C. monroi*, *C. uniflora*, *C. vexillata***

54	Pod valves obviously dehiscent at base, apex, and on lateral walls	*55*
55	Pods > 20 mm long	***C. williamsii***
55	Pods < 15 mm long	*56*
56	Seeds attached to funicle at pod dehiscence, seed remaining in pod	***C. appressa*, *C. australis*, *C. nana***
56	Seeds detaching from funicle at pod dehiscence, seed falling from the pod	***C. hollowayi*, *C. petriei***

PART II: PHYLOGENETIC ANALYSIS

Part II of this thesis is on the evolution and phylogeny of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. To provide new characters of systematic importance for the phylogenetic part of the study new information on wood anatomy (Chapter 4) and heteroblasty (Chapter 5) is presented. The phylogenetic methods of analysis, the plant species studied, and the selection of characters are presented in detail in Chapter 6.

CHAPTER FOUR

ANATOMY

4.1 INTRODUCTION

Comparative wood anatomy has been used extensively in the last 100 years to provide an indication of relationships among flowering plants at generic, family, and order levels (Solereder 1908; Carlquist 1988). Wood characters of systematic value tend to be those that are conservative and therefore occur throughout a taxon, and these usually have had a marked selective value in the early evolution of the group. However, caution is needed as some characters are essentially relictual and are not of systematic value, and these often occur in groups that are not closely related. Wood features can also evolve at different rates and also in response to different ecological conditions. Care is often needed in the selection of wood features as they may be relatively uniform throughout a family, or different among species of the same genus, phenotypic and genotypic variation occurs, and some wood features are more sensitive indicators of ecology than systematic relationships (Carlquist 1988).

Wood features of systematic value at generic and family rank can include vessel grouping, perforation plate type, lateral wall pitting of vessels, vesturing, helical sculpture, imperforate tracheary elements, axial and ray parenchyma, and cells contents and secretory glands (Carlquist 1988).

The general wood anatomy of the Fabaceae subfamily Faboideae has been described by Solereder (1908) and Metcalfe & Chalk (1950), both as Leguminosae subfamily Papilionaceae. Additional characters have been noted by Reinders-Gouwentak & Rijsdijk (1955). Summaries of the wood anatomy of the Fabaceae have been provided by Baretta-Kuipers (1981) and Wheeler & Baas (1992), and the wood anatomy of various genera of the Faboideae from Israel (Fahn et al. 1986) and Europe (Schweingruber 1990) has also been described and illustrated. The majority of the woody Fabaceae have diffuse porus wood, vessels with simple perforation plates, vestured alternate intervessel pitting, vessel-ray pitting of the same size, and calcium oxalate crsytals in chambered axial parenchyma cells (Gasson 1994).

Wood anatomy of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and

Notospartium has received very little attention. The first description was of an unknown species of *Carmichaelia* by Solereder (1908), who noted that the vessels had helical thickenings and are in groups, and that the rays are 8 cells wide. Metcalfe & Chalk (1950) described a young stem of *Carmichaelia australis* as having vessels in tangentially extended clusters and they confirmed the walls had helical thickenings. Slade (1952) studied the cladodes of several species of the *Carmichaelia* complex, but gave particular emphasis to the leaf trace systems. More recently, helical thickenings, vestured pits, simple perforation plates (Meylan & Butterfield 1974, 1975, 1978; Ohtani et al. 1984), and warts (Ohtani et al. 1983) have been observed in the vessels of several species of *Carmichaelia*, *Chordospartium stevensonii*, *Corallospartium crassicaule*, and *Notospartium carmichaeliae*.

Wood anatomical features have been shown to have a correlation to a species habitat (Carlquist 1975, 1977a, 1977b, 1977c, 1988; Carlquist & DeBuhr 1977; Baas et al. 1983; Baas & Schweingruber 1987). In particular, features of the vessel elements can often be matched to a specific habitat type. Species usually occurring in xeric habitats have shorter and narrower vessel elements and more vessels per mm^2 than those of mesic habitats. Such vessel elements are considered by Carlquist (1977b) to be more resistant to collapse or deformation than long vessel elements because of the strengthening furnished by the end walls. Numerous vessels per mm^2 provide conductive safety by ensuring that air embolisms formed under water stress do not seriously impair the conductive efficiency of a plant (Carlquist 1988). The vessel characteristics of diameter, length, and number per mm^2 have been used to produce indices of vulnerability and mesomorphy which allow an assessment of the relationship between wood anatomy and ecology (Carlquist 1977c; Carlquist & DeBuhr 1977). If vulnerability is less than 1 or mesomorphy below 75 the taxon is considered to be suited to xeric conditions (Carlquist 1977b). Diagonal vessel aggregations and vasicentric tracheids are also features of some woods from xeric habitats (Carlquist 1984, 1987). Although the vulnerability and mesomorphy indices have been criticised (Van den Oever et al. 1981; Baas 1986) their use permits comparison with plants from arid regions and it facilitates comparison among species of the *Carmichaelia* complex.

The wood anatomy study was initiated in an attempt to identify characters that would be useful in assessing the systematic and phylogenetic relationships among *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. The significant

variation in growth habit and extent of woodiness among the four genera suggested that there could also be anatomical differences. The relationship between species wood anatomy and habitat preferences are investigated, with the broad aim of understanding different species evolutionary ecology and the whether there is an ecological basis for variation in some wood characters.

4.2 MATERIALS AND METHODS

The wood anatomical descriptions and discussion are based on the material listed in Appendix 2, and includes eight species of *Carmichaelia*, the single species of *Corallospartium*, and all species of *Chordospartium* and *Notospartium*. The taxonomy of *Carmichaelia* and *Notospartium* is based on the revision presented in Chapter 3 and that of *Chordospartium* follows Purdie (1985). Voucher specimens supporting the wood samples are deposited in the herbarium (CHR) of Landcare Research, Lincoln, New Zealand. For each plant one transverse disc was obtained from the main stem or a main branch. Two blocks of wood for sectioning were selected from peripheral positions in each disc. Radial and tangential chips were removed from each block of wood for maceration. The following measurements and counts were made from the material prepared from each block: vessel number per mm^2 (6 counts), vessel number per group (25 counts), vessel element lengths and tangential diameter (25 counts), and the length of fibres, ray width, and height of multiseriate rays (each 25 counts). The main cell types (vessels, fibres, and ray and axial parenchyma) were examined in transverse, radial, and longitudinal sections as this ensured that any anatomical variation would be identified and its systematic or ecological significance evaluated.

Laboratory procedures used were similar to those described by Patel (1973). An additional procedure to prevent transverse sections rolling up after they had been removed from the wood block was to press the sections firmly between glass slides and then boil them for between 3-4 hours. Standard procedures were used for the preparation of specimens for the SEM (e.g., Exley et al. 1974, 1977).

The vulnerability indices were calculated by the mean vessel diameter being divided by the mean vessel number per mm^2, and the mesomorphy indices were calculated by multiplying the vulnerability index by the mean vessel element length (Carlquist 1977c; Carlquist & DeBuhr 1977).

ANOVA and Scheffe's Multiple Comparison test (95% confidence limits) were conducted to evaluate variation of six quantitative wood characters: vessel diameter, vessel length, the number of vessels per group, ray width, ray height, and fibre length. The raw data for these characters is presented in Appendix 3.

Terminology generally follows Wheeler et al. (1989) unless otherwise stated. For some other features I have followed Carlquist (1988), for example, vessel aggregations (p. 49-52) and vascular and vasicentric tracheids (p. 133-135).

4.3 WOOD ANATOMY

The following is a general description of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. The density and dimensions of vessels, rays, and fibres are given in Table 4.1.

WOOD diffuse porous (Fig. 4.1), semi-ring-porous (Fig. 4.2-4.6, 4.8, 4.9), or ring-porous (Fig. 4.7).
GROWTH RINGS distinct (Fig. 4.2, 4.3, 4.5-4.9) to poorly defined (Fig.4.4)
VESSELS in clusters (Fig. 4.8, 4.9), occasionally solitary (Fig. 4.1), often forming distinctive tangential, diagonal, radial, and dendritic aggregations (Fig. 4.2, 4.5, 4.6, 4.7), but these patterns sometimes absent from some very narrow growth rings (Fig. 4.4, 4.5), tangential bands often pronounced (Fig. 4.7); narrow diameter latewood and intermediate wood vessels usually in clusters or aggregations formed from radial multiples (Fig. 4.8, 4.9); small diameter vessels often associated with larger clusters of larger diameter vessels (Fig. 4.10); outline circular to polygonal (Fig. 4.8, 4.9, .4.10); elements storied (Fig. 4.11, 4.12), storeying sometimes irregular (Fig. 4.13, 4.14); mean = 735/mm^2 (range = 84-3704), mean tangential diameter 25.6 μm, mean elements length 121 μm (range = 45-315); perforation plates simple (Fig. 4.15, 4.16), circular or oval, outline sometimes irregular, usually terminal but sometimes lateral; intervessel pits 4-21 μm in diameter, often elongated (Fig. 4.15), mainly alternate (Fig. 4.17, 4.18, 4.19, 4.20), sometimes transitional on narrow elements, angled when crowded (Fig. 4.17, 4.18), circular when not crowded (Fig. 4.19), vestured; helical thickenings present in all elements (Fig. 4.21, 4.22); tyloses absent; pits to rays bordered (Fig. 4.23), vestured, 4.5-7.5 μm in diameter.

Table 4.1 Frequency and dimensions (including standard deviation) of vessels, rays, and fibres, and vulnerability and mesomorphy indices.

	Vessels						
	Number/mm^2		Diameter (μm)		Length (μm)		V/G
Species	Range	Mean	Range	Mean	Range	Mean	Mean
Ca. australis	148-384	238±94a	10-50	28±8.6b	82-175	136±21.2bcd	15.2±13.3a
Ca. compacta	804-1452	1148±247ab	12-52	28±9.3b	55-160	109±24.4ab	15.6±15.5a
Ca. corrugata	556-1524	1132±336ab	12-42	28±8.6b	87-315	153±41.6cd	12.1±12.1a
Ca. monroi	528-2064	1133±581ab	12-42	25±7.5ab	47-297	153±68.9cd	14.2±20.9a
Ca. nana	832-3704	1800±872b	5-37	18±7.1ab	60-140	97±16.2a	14.2±11.3a
Ca. odorata	100-208	162±39.4a	11-70	33±15.4c	125-215	161±22.2cd	7.1±5.2a
Ca. petriei	1096-2028	1552±316b	10-52	20±9.6ab	45-140	96±16.2a	18.3±14.8a
Ca. williamsii	84-216	133±48a	12-52	33±8.7c	100-180	138±17.4bcd	6.3±3.8a
Ch. muritai	104-440	205±108a	9-57	27±10.8b	90-180	136±17.8bcd	9.1±5.8a
Ch. stevensonii	172-480	285±99a	10-40	21±7.2ab	80-175	142±47.2bcd	13.2±6.4a
Co. crassicaule	1184-2592	1660±448b	6-22	15±4.2a	72-172	111±20.5ab	49.5±37.2b
N. carmichaeliae	216-416	320±70.7a	10-70	27±12.7b	55-180	136±25bcd	14.4±11.0a
N. glabrescens	156-288	231±49a	9-70	29±13.4b	70-160	117±16.5abc	13.2±10.5a

N. torulosum	140-568	317±117a	10-57	26±11.7ab	65-155	117±18.8abc	16.7±8.6a
All samples	84-3704	709±694	5-70	25.5±11.4	45-315	114±50.8	14.7±16.2
ANOVA		$F_{13,102}$=29.87		$F_{13,930}$=19.59		$F_{13,985}$=36.53	$F_{13,550}$=16.11
		$P = 0$		$P = 0$		$P = 0$	$P = 0$

Legend: V/G = mean number of vessels per group.

Table 4.1 (cont.) Frequency and dimensions (including standard deviation) of vessels, rays, and fibres, and vulnerability and mesomorphy indices.

	Rays				Fibres		Ecological indices	
	Height (μm)		Width (cells)	Type	Length (μm)			
Species	Range	Mean	Mean		Range	Mean	Vuln.	Meso.
Ca. australis	175-2200	792±429a	7.2±3.3	het.	570-1510	1020±194bcdef	0.109	14.7
Ca. compacta	110-2660	711±519a	6.6±3.5	het.	330-1210	702±210a	0.024	2.6
Ca. corrugata	162-10135	2104±640b	6.0±3.1	het	630-2320	1360±306g	0.025	3.8
Ca. monroi	200-2590	848±488a	6.3±4.5	het.	660-1670	1226±301fg	0.022	3.3
Ca. nana	94-1351	409±238a	5.7±4.9	het	500-1932	1056±228cdef	0.010	0.9
Ca. odorata	229-1540	785±293a	7.4±3.4	het.	405-1337	901±245abcde	0.200	32.2
Ca. petriei	148-2229	590±358a	10.3±4.1	het.	493-1243	886±175abcde	0.013	1.2
Ca. williamsii	128-2580	716±4.8a	8.5±3.6	het.	420-1510	1123±244cefg	0.248	34.2
Ch. muritai	121-1905	653±303a	8.2±3.9	ho.	472-1108	826±134ab	0.131	17.8
Ch. stevensonii	90-1250	599±353a	5.7±1.8	ho.	590-1440	1037±158bcdef	0.073	10.4
Co. crassicaule	148-2480	775±488a	6.3±5.3	het.	440-1210	817±202ab	0.009	1.0
N. carmichaeliae	175-1581	660±373a	6.6±3.3	ho.	472-1337	895±189abcde	0.084	11.4
N. glabrescens	162-2729	620±375a	8.0±3.4	ho.	432-1283	918±166abcde	0.125	14.6

N. torulosum	135-1040	673±313a	7.2±2.9	ho.	554-1405	868±170abd	0.082	9.6
All samples	90-10135	622±738	7.1±3.8	-	330-2320	839±432	0.083	11.15
ANOVA		$F_{13,946}$=15.84	$F_{13,505}$=5.01			$F_{13,985}$=46.79		
		$P = 0$	$P < 0.0001$			$P = 0$		

Legend: het. = ray body cells all heterogeneous; ho. = ray body cellsall homogeneous.

VASICENTRIC AND VASCULAR TRACHEIDS occasionally present (Fig. 4.24) or absent; intergrading with narrow vessel elements; storied; pits vestured; helical thickenings present.

AXIAL PARENCHYMA abundant to occasionally present; commonly to rarely vasicentric, sometimes confluent and forming irregular bands, diffuse, and sometimes diffuse-in-aggregates; following radial and tangential vessel patterns; with gable-ends on the tangential face (Fig. 4.11, 4.12, 4.27); in latewood and intermediate wood (when associated with narrow vessel elements) usually in radial multiples; predominantly storied; storied fusiform cells common, and storied strands of 2 ordinary cells also present; non-storied fusiform and non-storied parenchyma strands with 2-4(-9) ordinary cells absent or rare; disjunctive cells present (Fig. 4.25).

RAYS 1-20 cells wide (Fig. 4.26, 4.27, 4.28, 4.29, 4.30); tails of 1-7 cells (Fig. 4.26) rare to very rare; body ray cells exclusively procumbent (Fig. 4.31, 4.32), or mainly procumbent but with some square and upright cells (Fig. 4.33, 4.34, 4.36); procumbent marginal cells often narrower than procumbent body cells (Fig. 4.12, 4.31), or sometimes square and upright; short narrow rays sometimes storied; dissected rays sometimes present (Fig. 4.35, 4.36); dimorphic rays sometimes present (Fig. 4.37); sheath cells absent to frequent (Fig. 4.27); disjunctive cells present; cells with simple perforations very rare (Fig. 4.38).

FIBRE TRACHEIDS 50-70 μm long, 4-6 μm wide, occasional; bordered pits 1.5-2.25 μm in diameter (Fig. 4.39, 4.40); helical thickenings absent; vestured (Fig. 4.40); non-septate.

FIBRES thick to very thick walled, occasionally to often gelatinous (Fig. 4.8, 4.9, 4.10), with minute slit-like pits generally in radial walls.

4.3.1 Wood and growth rings

Chordospartium, *Corallospartium*, *Notospartium*, and most species of *Carmichaelia* have semi-ring-porous wood (Fig. 4.2-4.6, 4.8, 4.9). In these, growth ring boundaries are marked by large diameter earlywood vessels and narrow diameter latewood vessels. *Carmichaelia williamsii* has diffuse porous wood and lacks obvious growth ring boundaries (Fig. 4.1). Ring-porous wood occasionally occurs in *N. carmichaeliae* (Fig. 4.7).

The presence of distinctive clusters of narrow diameter vessels in latewood and

sometimes in intermediate wood of one growth ring, when compared with the obvious large diameter earlywood vessels of an adjacent growth ring, can sometimes give the impression of ring-porous wood. This pattern is usually seen in narrow growth rings when the large diameter vessels in earlywood occur in tangential rows 1-2(-3) vessels wide, and adjacent to these are small latewood vessels (Fig. 4.4).

4.3.2 Vessels

The mean number of vessels per group varies from 6.3 (range 1-16) in *Ca. williamsii* and 7.1 (1-20) in *Ca. odorata* to 49.5 (8-185) in *Co. crassicaule*. The other species studied have a mean number of vessels per group of between 9.1 and 18.3 (1-67). In *Co. crassicaule* the large areas of fascicular tissue comprising numerous small diameter vessels and few axial parenchyma cells (Fig. 4.6) accounts for the high number of vessels per group. *Co. crassicaule* differs significantly from all other species in its number of vessels per group (Table 4.1; Fig. 4.41). Clusters of small diameter vessels aligned in radial multiples are a prominent feature of the latewood of *Ca. australis* (Fig. 4.9), *Ca. compacta*, *Ca. nana*, *Ca. petriei*, *Co. crassicaule* (Fig. 4.8), *Chordospartium*, and *Notospartium*.

The mean number of 709 vessels per mm^2 is very high, and this is because of the vessels having a narrow diameter and the large number of vessels per group. *Carmichaelia williamsii* and *Ca. odorata* have the lowest number of vessels per group and the lowest number of vessels per mm^2. *Corallospartium crassicaule* with a mean of 1660 vessels per mm^2 and a mean of 49.5 vessels per group, has only a few large vessel groups per mm^2. Although *Ca. nana* has a similar number of vessels per mm^2 it has only 14.2 vessels per group and therefore more vessel groups per mm^2. It is interesting that *Ca. nana* sample 4 averages 2693 vessels per mm^2, which is one of the highest vessel densities ever recorded. The three counts for sample 4 are 1644, 2732, and 3704. The mean for the four samples of *Ca. nana* is 1800. Previously, Wallace (1986) reported 2673 vessels per mm^2 for a single plant of *Cassiope fastigiata* (Ericaceae). Variation in the number of vessels per mm^2 is very significant, with two groups being recognised (Table 4.1). *Co. crassicaule*, *Ca. nana*, *Ca. petriei*, *Ca. compacta*, *Ca. corrugata*, and *Ca. monroi* are very similar in having a high number of vessels per mm^2, although the latter three species also overlap with the other species which have a lower vessel density (Table 4.1).

In *Chordospartium*, *Notospartium*, and *Ca. odorata*, vessels are often in clusters aligned in tangential bands (Fig. 4.7), as well as in diagonal aggregations. In *Corallospartium* and the other species of *Carmichaelia* the vessels are mainly in clusters or diagonal aggregations, and when tangential bands are present they intergrade with diagonal aggregations. Diagonal vessel grouping is often a characteristic of woods from drier and colder localities (Carlquist 1987).

In all species earlywood vessel groups have fewer vessels than latewood groups (Fig. 4.8, 4.9). Large diameter earlywood vessels are invariably associated with a similar number of smaller diameter vessels (Fig. 4.10). Comparison of large diameter earlywood vessels and narrow diameter latewood vessels is made by comparing latewood vessels of one growth ring with earlywood vessels of another growth ring (Fig. 4.8, 4.9). The diffuse-porous wood of *Ca. williamsii* lacks obvious growth ring boundaries and clusters of vessels are uniformly scattered across the transverse section (Fig. 4.1).

The mean vessel diameter of all samples is 25.5 μm, with a range of 5-70 μm between the large diameter earlywood vessels and narrow diameter latewood vessels. Very narrow diameter vessels are also often associated with large earlywood vessels (e.g., Fig. 4.10). In *Ca. odorata*, *N. carmichaeliae*, and *N. glabrescens* the widest earlywood vessel diameter is 70 μm, whereas in *Co. crassicaule* and *Ca. nana* the widest diameter is 22 μm and 37 μm respectively. *Carmichaelia williamsii* has the highest mean vessel diameter at 33 μm, and *Co. crassicaule* the lowest at 14 μm. Variation in vessel diameter is highly significant, with *Ca. odorata* and *Ca. williamsii* having larger diameter vessels than a number of other species, including *Co. crassicaule*, *C. nana*, and *Ca. petriei* (Table 4.1; Fig. 4.42).

Mean vessel element length is 114 μm, with a range between 96 μm for *Ca. petriei* and 161 μm for *Ca. odorata*. Variation in vessel length is highly significant, and a number of distinct groups are recognised (Table 4.1; Fig. 4.43). *Ca. nana* and *Ca. petriei* have particularly short vessels and can be distinguished from all other species (Table 4.1). No variation in length was observed between narrow latewood and wide earlywood vessels.

Intervessel pits in *Chordospartium*, *Corallospartium*, *Notospartium*, and *Ca. odorata* are often crowded and with an angular outline (Fig. 4.17), whereas in other species of *Carmichaelia* the pits are less crowded and the outlines are usually round or

oval. Transitional pitting (sensu Carlquist 1988, p. 74) occurs in some narrow vessel elements of *Co. crassicaule* and *Ca. nana*, and elongated pits are occasionally observed on wide vessels of most species (Fig. 4.15, 4.20).

Helical thickenings occur in all species, but are most pronounced in the dwarf shrubby *Ca. corrugata*, *Ca. monroi*, and *Ca. nana*. In *Ca. nana* the thickness of the helical thickenings in narrow vessels is 0.7-1.0 μm wide and in broad vessels it is 2.5-5.0 μm wide (Fig. 4.22). In the tall shrubby species of *Carmichaelia*, *Chordospartium*, and *Notospartium* helical thickening is generally narrow (1.2-1.6 μm) in all elements.

The diameter of the perforation plates varies with the diameter of the vessel. In narrow vessels perforation plates as small as 4.5 μm were observed. The perforation plates of narrow diameter vessels are often visible across a growth ring in radial longitudinal sections (Fig. 4.16). Vestured pits (Meylan & Butterfield 1974, fig. 25, 26) were observed in all species studied.

4.3.3 Vasicentric and vascular tracheids

Vasicentric tracheids were observed with certainty in *Ca. corrugata*, *Ca. compacta* (Fig. 4.24), and *Ca. monroi*. *Ca. corrugata* has numerous vasicentric and also a few vascular tracheids, whereas *Ca. compacta* and *Ca. monroi* have only a few vasicentric tracheids and possibly occasional vascular tracheids. The presence of vasicentric tracheids is most evident in macerations where their direct association with vessel elements can be clearly seen. Imperforate tracheary cells not associated with vessel elements are either vascular tracheids or vasicentric tracheids which have become disassociated from the vessels in the maceration preparation. Vasicentric tracheids in *Ca. compacta*, *Ca. corrugata*, and *Ca. monroi* have helical thickening.

Thorough searching of macerations of *Chordospartium*, *Corallospartium*, *Notospartium*, and the other species of *Carmichaelia* did not reveal the presence of vasicentric or vascular tracheids. These taxa all have numerous narrow vessel elements with very small perforations, but no imperforate tracheary cells with helical thickening and bordered pits were noted.

4.3.4 Parenchyma

Axial parenchyma is predominantly fusiform and storied in the *Carmichaelia* complex. Two cells per parenchyma strand (Fig. 4.11) are recorded for all species, and

they are either absent or present in low numbers in a given sample. Three cells per strand were rarely seen in *N. torulosum* and *Ca. corrugata*, and one strand with four cells was noted in *N. glabrescens*. In *Ca. corrugata* one strand with nine cells was observed as were several non-storied very long fusiform cells. Non-storied fusiform cells were also recorded for *Ch. muritai*.

In all species of *Carmichaelia* diffuse parenchyma is common, and diffuse-in-aggregates is usually present in *Ca. australis*, *Ca. compacta*, *Ca. corrugata*, *Ca. monroi*, and *Ca. petriei* but it was not often observed in *Ca. nana*, *Ca. odorata*, and *Ca. williamsii*. In *Corallospartium*, *Chordospartium*, and *Notospartium* diffuse and diffuse-in-aggregates parenchyma is not common, and in *N. carmichaeliae* diffuse parenchyma is virtually absent. *Corallospartium crassicaule* is readily recognised by scanty and diffuse parenchyma. Furthermore, ray adjacent parenchyma (Carlquist 1988) is particularly obvious in *Co. crassicaule*, although it is present in all species. Axial parenchyma in *Notospartium* and *Ch. muritai* is commonly vasicentric, and in *Ch. stevensonii* it is occasionally vasicentric.

Disjunctive axial parenchyma cells are reasonably common in all species (Fig. 4.25), and their presence is a further record for the Fabaceae.

The body ray parenchyma cells of *Chordospartium* and *Notospartium* are exclusively procumbent (Fig. 4.31, 4.32), whereas those of *Carmichaelia* and *Corallospartium* are predominantly procumbent but square and upright cells are also frequent (Fig. 4.33, 4.34, 4.36). Ray height is very similar for all species except *Ca. corrugata* which sometimes has very high rays (Table 4.1; Fig. 4.44).

In tangential longitudinal section the multiseriate rays of *Chordospartium*, *N. carmichaeliae*, and *N. torulosum* usually have small diameter ray cells on the margin, with large diameter cells comprising the ray body (Fig. 4.12). However, this pattern is not always present in these species and sometimes the different sized ray cells are mixed across the body and margin of the cell. *Notospartium glabrescens*, *Corallospartium*, and most species of *Carmichaelia* have small and large diameter cells intermingled throughout the ray margin and body (Fig. 4.13, 4.14). However, *Ca. compacta*, *Ca. nana*, and *Ca. williamsii* often have larger cells on the margin and smaller cells comprising the ray body (Fig. 4.28). In all species uniseriate rays consist of either exclusively small or large diameter cells, or both combined. Sheath cells are frequent in *Ca. odorata* sample 2 and *Ca. nana* sample 1 (Fig. 4.27), although in all other species

they are generally rare to very rare, and they were not seen in *Ca. corrugata*, *Ca. monroi*, and *Ca. crassicaule*.

Tails are generally only 1-3, but rarely up to 7 cells long, and although not particularly common they appear to be slightly more frequent in most species of *Carmichaelia* than in *Chordospartium*, *Corallospartium*, and *Notospartium*. Dissected rays (Fig. 4.35, 4.36) occur sparingly in all species, but are most common in *Ca. compacta*. There is often considerable variation in the width and shape of rays as is illustrated for *C. nana* (Fig. 4.26, 4.27, 4.28) and *N. glabrescens* (Fig. 4.29, 4.30). There is no significant variation in the width of rays (Fig. 4.45).

4.3.5 Fibre tracheids and fibres

Fibre tracheids are scattered amongst the axial parenchyma and fibres (Fig. 4.39) of all species. They are easily overlooked because of their small size and very narrow diameter, and they are best observed by searching for the small but usually conspicuous bordered pits (Fig. 4.40).

Gelatinous fibres (Fig. 4.8, 4.9, 4.10) were observed in all species, and while mostly occurring in inclined stems they were also observed on some vertical stems (e.g., *Ca. australis*, Fig. 4.9) which is likely to indicate wind thrashing. Abundant fibres in large diagonal aggregations are characteristic of *Co. crassicaule*, and fibres in pronounced tangential aggregations occur in *Chordospartium* and *Notospartium*. Most species of *Carmichaelia* have diffuse-in-aggregate fibres which are mixed in a random manner with groups of vessels and the axial parenchyma. Variation in fibre length is highly significant and can distinguish a number of species, although many of the species may belong to more than one group (Fig. 4.46). *Ca. compacta* with the shortest fibres and *Ca. corrugata* with the longest fibres are the most distinct species (Table 4.1).

4.3.6 Storied structure

Storied structure is characteristic of all four genera. In *Chordospartium* and *Notospartium* the storied structure is generally always obvious and well defined (Fig. 4.11, 4.12, 4.30) as the cells in a given bundle are very similar in length. In *Carmichaelia* and *Corallospartium* the storied structure is also obvious, but it is sometimes irregular and less well defined (Fig. 4.13, 4.14, 4.28). This is particularly so when two vascular bundles with different length vessel elements and parenchyma cells

join, and the combined bundle often has cells of the two different lengths.

4.4 DISCUSSION

Metcalfe & Chalk (1950) listed several wood anatomical characters which typically occur in woods of the Papilionaceae (= Fabaceae subfamily Faboideae). These features occur in the wood of the *Carmichaelia* complex and include strong vessel patterns, spiral thickening of vessels, axial parenchyma fusiform but sometimes with two cells per strand, a storied structure, predominantly heterogenous rays, and the aseptate fibres. Other wood characteristics of the Faboideae that occur in the *Carmichaelia* complex include vessels with simple perforations (Solereder 1908), and axial parenchyma with gable-ends on the tangential face (Reinders-Gouwentak & Rijsdijk 1955).

The wood anatomy of various genera of the Faboideae from Israel (Fahn et al. 1986) and Europe (Schweingruber 1990) has been described and illustrated, and many of these northern hemisphere species are remarkably similar to, and have several features in common with, species of the *Carmichaelia* complex. Some of the most obvious similarities are ring- to semi-ring-porous wood, vessels with helical thickenings, vessel elements in groups and in diagonal and dendritic aggregations, vasicentric parenchyma forming patterns with vessels, storied structure, and wide rays. Many of these features can be seen, for example, in *Cytisus scoparius*, *Genista aetnensis* (Schweingruber 1990), *Anagyris foetida*, and *Gonocytisus pterocladus* (Fahn et al. 1986).

Two groups within the *Carmichaelia* complex are distinguished by their ray type: *Carmichaelia* and *Corallospartium* have procumbent, square, and upright ray cells, and *Chordospartium* and *Notospartium* have procumbent ray cells. Kribs (1935) suggested that homogeneous rays are more advanced than heterogenous rays because they have lost the square and upright cells. However, such generalisations are difficult to apply universally given the many parallelisms and reversals in wood anatomical features (Baas & Wheeler 1996). In addition, *Carmichaelia* and *Corallospartium* often have slightly irregular storied structure, whereas *Chordospartium* and *Notospartium* have a well defined storied structure. The composition of these two groups contrasts with other features which are in different combinations among the four genera. For

example, *Chordospartium* and *Corallospartium* have small, similarly shaped, indehiscent, and mainly 1 seeded pods, and unilocular anthers are a feature of *Carmichaelia* whereas bilocular anthers occur in *Chordospartium*, *Corallospartium*, and *Notospartium* (Godley 1980). Furthermore, Heenan (1997) has reported that several features associated with heteroblastic development occur in different combinations among the four genera. Some of the wood anatomy features reported here are to be included with characters from morphology, floral biology, fruit anatomy, and heteroblasty in a cladistic analysis of the Australian and New Zealand genera *Carmichaelia*, *Chordospartium*, *Corallospartium*, *Notospartium*, *Clianthus*, and *Swainsona*.

Adult plants of *Chordospartium*, *Corallospartium*, *Notospartium*, and most species of *Carmichaelia* are leafless, or almost leafless, a condition suggesting they are suited to low rainfall areas and/or drought prone sites such as thin soils or coarse gravels. The wood anatomy of the *Carmichaelia* complex is also distinctly xeromorphic, having conductive safety in the form of vessel elements that are narrow and short, and with numerous vessels per mm^2 of transection (Table 4.1). The mean vessel element diameter of 25.6 μm is very low in terms of world figures and is comparable with desert scrub (25.9 μm) and alpine plants (20.9 μm) from southern California (Carlquist & Hoekman 1985), and it is lower than Australian shrubs from coastal (41 μm), desert (37 μm), and sand heath (33 μm) habitats (Carlquist 1977b). However, vessel diameter means for species of the *Carmichaelia* complex do not reflect the actual range of diameters (Table 4.1), and large diameter and narrow diameter size classes occur in ring- and semi-ring-porous woods of the *Carmichaelia* complex (e.g., Fig. 4.7). Wide diameter earlywood vessels are efficient at water transport but vulnerable to embolisms, whereas the numerous narrow diameter vessels enhance conductive safety by providing protection against embolisms. Therefore, the presence of wide diameter and narrow diameter vessels is functionally and ecologically more important than the average vessel diameter (Baas et al. 1983). Similar size class differences are also a feature of the Fabaceae subfam. Faboideae and of species from xeric regions in Europe (Baas & Schweingruber 1987).

The mean vessel element length of 121 μm is also exceptionally low, and is most comparable with Israeli (121 μm) (Baas & Carlquist 1985) and southern Californian halophytes (100 μm) (Carlquist & Hoekman 1985). The mean vessel

element length of southern Californian and Australian desert shrubs is 190 and 218 μm, respectively. The mean number of vessels per mm^2 of transection (735) is also very high by world standards: arctic shrubs have 559 vessels per mm^2 (Carlquist 1977b) and southern Californian alpine shrubs have 442 vessels per mm^2 (Carlquist & Hoekman 1985). The number of vessels per group (15.6) is also high. In comparison, *Cassiope* with 1904 vessels per mm^2 has only 1.5 vessels per group (Wallace 1986) and, in the southern Californian flora, coastal sage species have 7.55 vessels per group, chaparral vegetation species have 4.76, and alpine species have 2.53 (Carlquist & Hoekman 1985).

The *Carmichaelia* complex vulnerability and mesomorphy values are exceptionally low (Table 4.1) and well within the ranges suggested by Carlquist (1977b) for xeromorphic woods: vulnerability < 1, mesomorphy < 75. The mean vulnerability (0.083) and mesomorphy (11.15) indices are most similar to both desert (V = 0.08; M = 17) and arctic (V = 0.10; M = 25) shrubs (Carlquist 1977b). The vulnerability and mesomorphy values can be correlated with species ecological preferences, and the specific sites from which the study plants were collected. For example, *Ca. nana* has one of the lowest vulnerability (0.010) and mesomorphy (0.9) values and it occurs in low rainfall areas of the central South Island on extremely dry and drought prone alluvial river beds and braid islands, river terraces, moraines and shingle slopes (Heenan 1995b). The samples of *Ca. nana* were collected from alluvial river terraces (samples 1 and 4) and loose shingle slopes (samples 2 and 3). *Corallospartium crassicaule* also has exceptionally low vulnerability and mesomorphy values and it too is often found on well-drained sites such as rock outcrops and old moraine surfaces.

Carmichaelia odorata and *Ca. williamsii* have the highest vulnerability and mesomorphy values (Table 4.1), but they are still considered to be xeromorphic because vulnerability is less than 1 and mesomorphy less than 75 (Carlquist 1977b). *Carmichaelia odorata* occurs in higher rainfall areas in the South Island along the northern half of the Main Divide and in the lower North Island mountains, and it is frequently associated with rivers and streams where it occurs on low terraces, riverbed flats, and forest margins (Heenan 1996a). *Carmichaelia williamsii* is from northern New Zealand, and is most common on the Poor Knights Islands and the Alderman Islands. *Carmichaelia williamsii* has diffuse porous wood, predominantly large diameter vessels, and very few clusters of only narrow diameter vessels. However, *Ca.*

williamsii does have conductive safety in that the vessel aggregations include both larger and smaller diameter vessels.

The often large clusters of narrow diameter latewood vessels which occur in predominantly diagonal aggregations in the *Carmichaelia* complex are also considered to be adaptations to a xeric environment (Carlquist 1987). These vessel clusters are more common in *Ca. compacta*, *Ca. petriei*, *Ca. nana*, and *Co. crassicaule* which occur in low rainfall areas and/or on drought prone sites, than in *Ca. australis* and *Ca. odorata* which occur in slightly more mesic situations. Vasicentric tracheids are also thought to be a drought survival mechanism in providing conductive safety (Carlquist 1985), and their relative abundance in *Ca. corrugata* could be related to its growth habit and habitat. This species is a strongly rhizomatous subshrub forming mats up to 1 m in diameter, with small stems up to 5 mm in diameter, and it occurs on gravel and sand soils, stone and gravel ridges and terraces, and dry sandy hummocks on terraces and river beds (Heenan 1995b).

I infer from the strongly xeromorphic wood of the *Carmichaelia* complex that the group is suited to low rainfall areas and drought or frost prone habitats, but it also suggests that the group may have radiated during periods of exceptionally dry, drought prone, or cold conditions. These conditions were present from Late Miocene time through the development of a major Antarctic ice cap (Kemp 1978), and a major lowering of temperatures in New Zealand that took place in the Late Pliocene (Kennett et al. 1971), and continued into the Pleistocene and Holocene. For example, during the coldest phase of the Holocene Otira Glaciation (18-20,000 yrs ago) mean temperatures were about 4.5°C lower than today in the central South Island (Soons 1979). However, Wardle (1988) believes that conditions were more severe than the estimation of mean temperature suggests, and that temperature inversions following passages of cold air would have been intense, and frost probably exceeded the cold tolerance of all but the hardiest plants.

By Late Pliocene the Kaikoura Orogeny had substantially uplifted the Southern Alps (Suggate et al. 1978), and glaciation and erosion of these mountains created new habitats such as outwash fans, terrace complexes, alluvial plains, and glacial moraine. At this time subarid areas were probably formed in the interior of the South Island (Raven 1973). Species such as *Ca. corrugata* and *Ca. nana* have very low vulnerability and mesomorphy values, and frequently occur on dry plains and terraces which are

drought and frost prone. *Carmichaelia petriei* occurs throughout Otago and displays considerable variation, sometimes over rather short distances (Heenan 1996a). Plants of *Ca. petriei* from the semiarid McKenzie Basin and upper Waitaki River are notable for their stout, pungent tipped, and yellow-green cladodes, and their wood also exhibits marked xeromorphic characteristics. Tolerance of cold and dry conditions and the nitrogen-fixing abilities of species of *Carmichaelia* may have made them important components of the vegetation on newly formed and disturbed surfaces during the Pliocene and Pleistocene.

The differences between *Ch. stevensonii* and *Ch. muritai* suggests that these species have slightly different habitat preferences, and this has some conservation implications. *Chordospartium muritai* is known from about 28 individuals in the wild, and it has been the subject of revegetation efforts in Marlborough at Clifford Bay, Marfels Beach, and in the Little Haldon Hills. *Chordospartium muritai* has fewer vessels per mm^2 of transection, a larger mean vessel diameter, fewer vessels per group, and higher vulnerability and mesomorphy values when compared to *Ch. stevensonii*. These features suggest that *Ch. muritai* occurs on slightly more mesic sites than *Ch. stevensonii*. This is significant as the single natural population of *Ch. muritai* grows on a deeply eroded cliff of coarse outwash gravels (Purdie 1985) prone to severe seasonal drought and may not be a typical or optimal habitat for the species. However, if the habitats of *Ch. stevensonii* could be clearly defined, and if these could be interpreted with features of wood anatomy, then by way of comparative ecology and wood anatomy it may be possible to select suitable sites for conservation plantings of *Ch. muritai*.

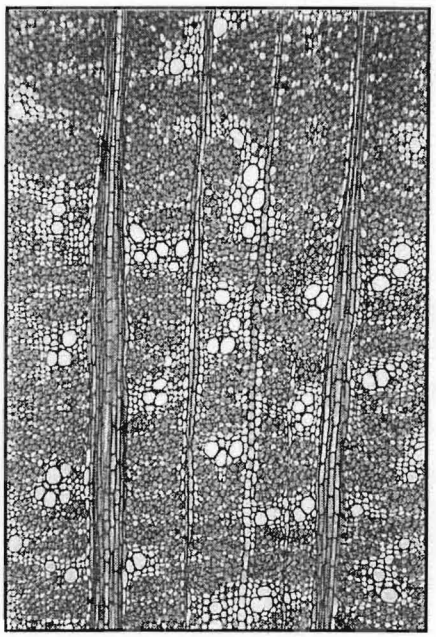


Figure 4.1

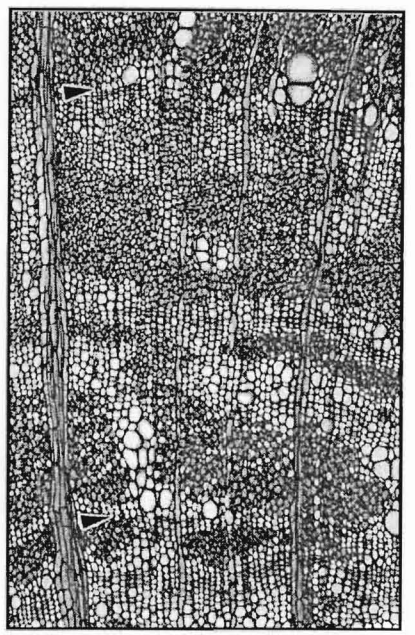


Figure 4.2

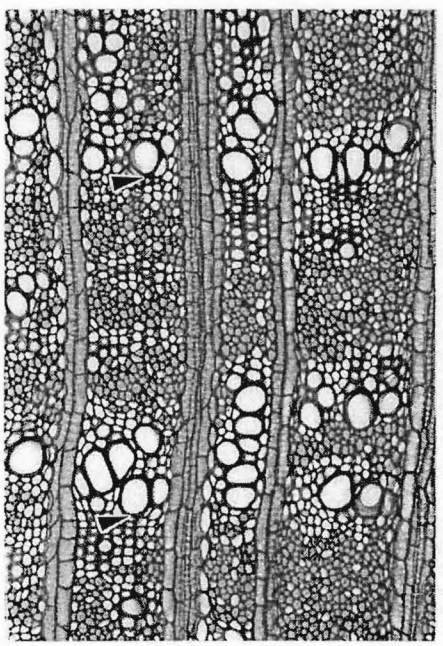


Figure 4.3

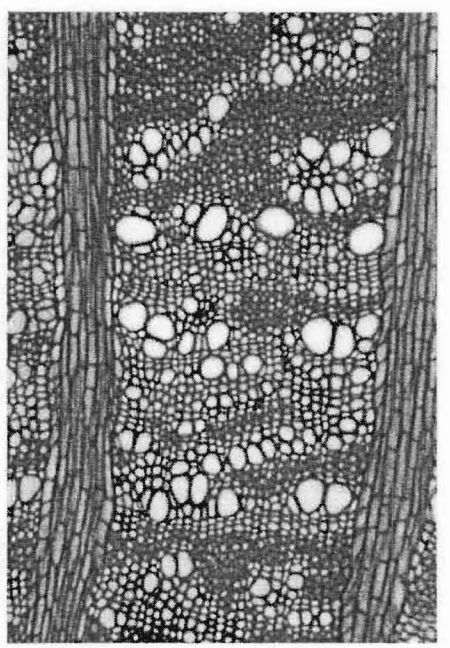


Figure 4.4

Fig. 4.1 *Ca. williamsii*. TS ×50. Wood diffuse-porous, and lacking growth ring boundaries. **Fig. 4.2** *Ca. nana*. TS ×80. Wood semi-ring-porous. Vessels in diagonal aggregations. Distinct growth ring boundaries at the top and bottom (arrows). **Fig. 4.3** *Ca. monroi*. TS ×100. Wood semi-ring-porous. Two distinct growth ring boundaries (arrows). Latewood vessel aggregations in radial multiples. **Fig. 4.4** *Ca. monroi*. TS ×100. Crowded and often poorly defined growth ring boundaries.

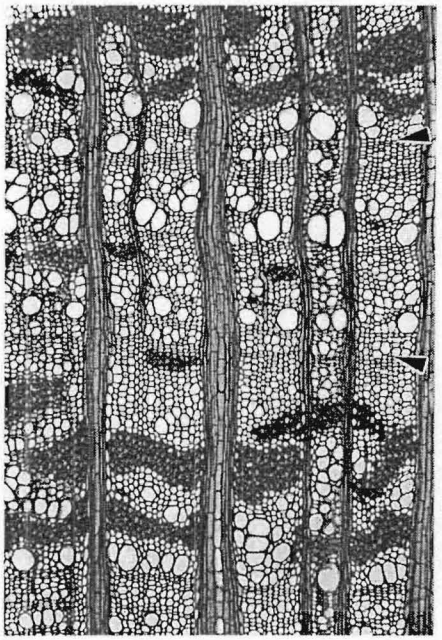
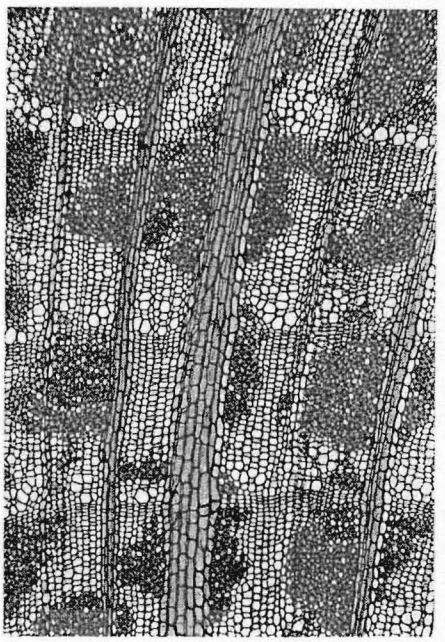


Figure 4.5



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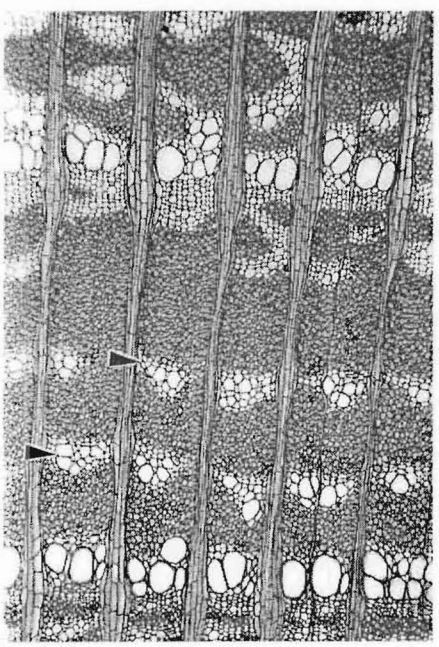


Figure 4.7

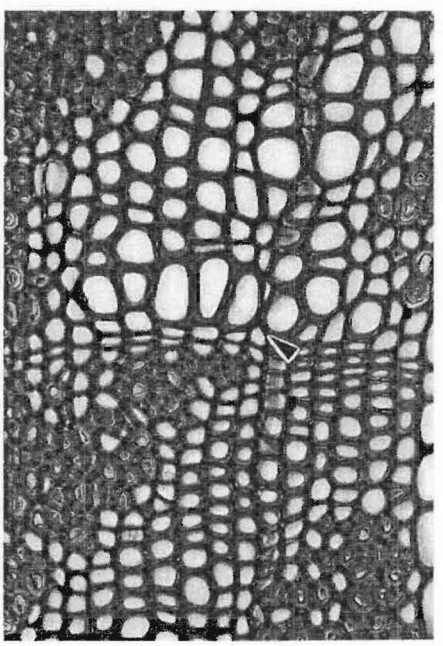


Figure 4.8

Fig. 4.5 *Ch. muritai*. TS ×50. Wood semi-ring-porous. Cluster of narrow growth rings (between arrows). **Fig. 4.6** *Co. crassicaule*. TS ×80. Wood semi-ring-porous Vessels in radial multiples, and in mostly radially orientated aggregations. **Fig. 4.7** *N. carmichaeliae*. TS ×50. Wood ring-porous and with two distinct growth rings. Note the vessels in tangential (arrows) and diagonal aggregations. **Fig. 4.8** *Co. crassicaule*. TS ×320. Growth ring boundary seen at centre (arrow), and note the gelatinous fibres. Compare with Fig. 4.9.

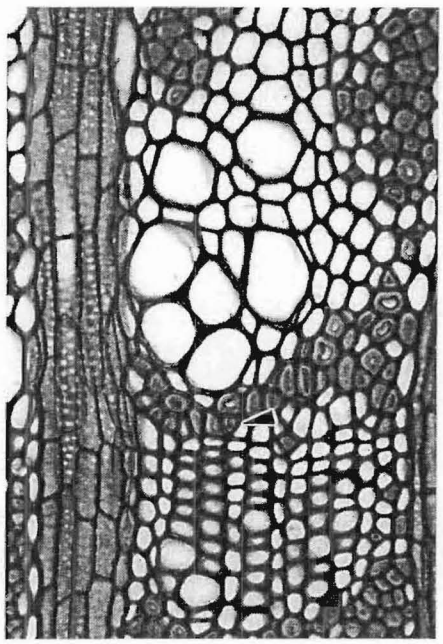


Figure 4.9

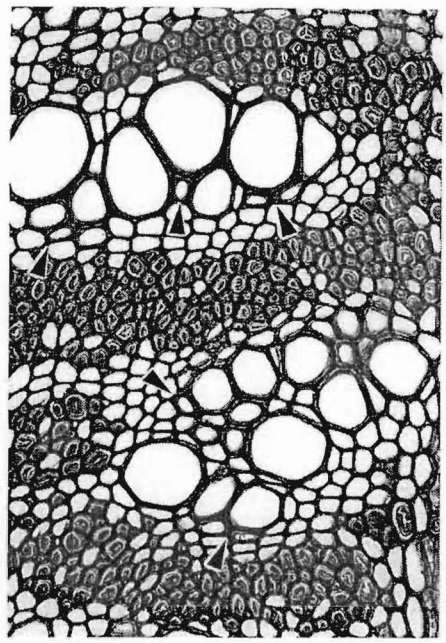


Figure 4.10

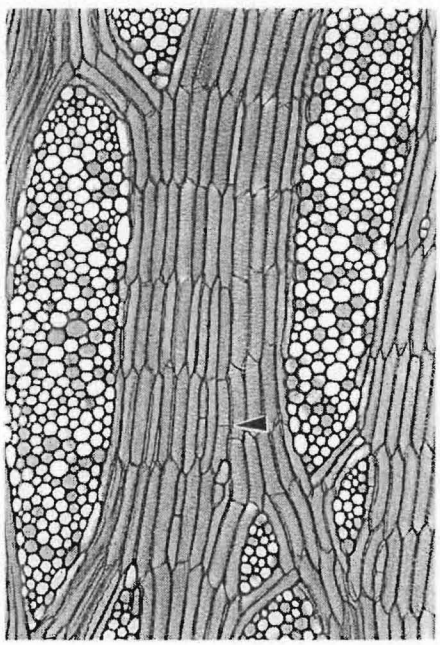


Figure 4.11

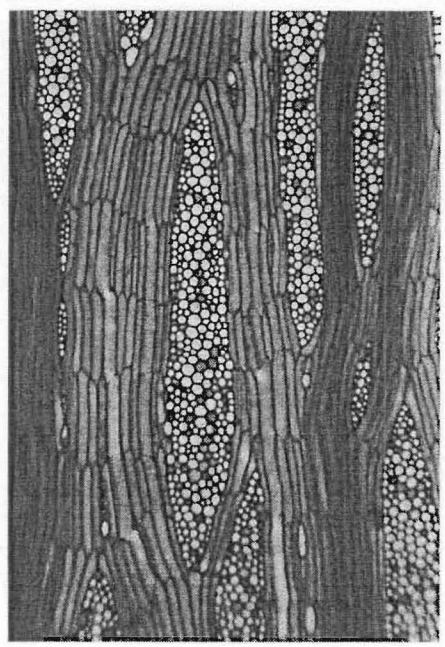


Figure 4.12

Fig. 4.9 *Ca. australis.* TS ×200. Growth ring boundary seen at centre (arrow) between few large diameter earlywood and numerous small diameter latewood vessels. Note the gelatinous fibres. Compare with Fig. 4.8. **Fig. 4.10** *Ca. odorata.* TS ×200. Few smaller diameter vessels (arrows) associated with two clusters of large diameter vessels. **Fig. 4.11** *N. torulosum.* TLS ×100. Prominent storied structure of axial parenchyma. Note two celled parenchyma strands (arrow) and gable ends of the parenchyma cells. **Fig. 4.12** *Ch. stevensonii.* TLS ×80. Prominent storied structure. Rays with small diameter marginal cells and large diameter body cells.

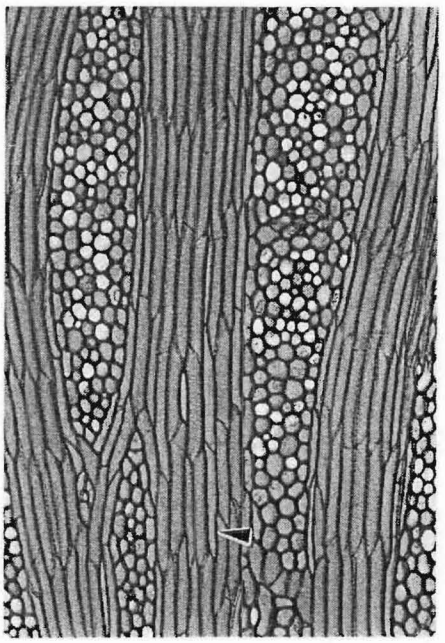


Figure 4.13

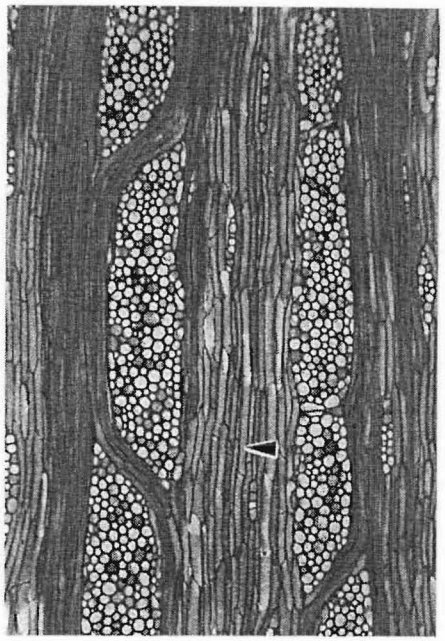


Figure 4.14

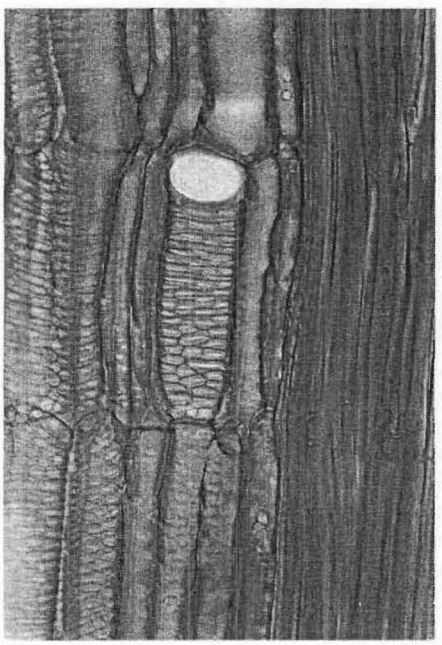


Figure 4.15

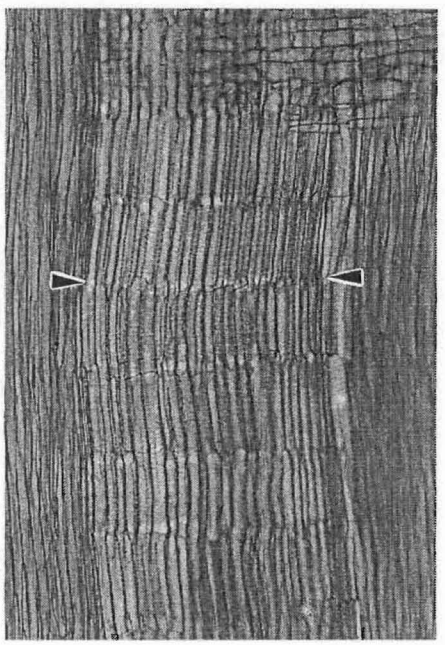


Figure 4.16

Fig. 4.13 *Co. crassicaule*. TLS ×128. Storied structure present, but poorly defined in places (arrow). **Fig. 4.14** *Ca. compacta*. TLS ×80. Storied structure present, but slightly irregular in places (arrow). **Fig. 4.15** *Ch. muritai*. TLS ×320. Simple perforation. Vessel pits elongated. **Fig. 4.16** *Co. crassicaule*. RLS ×100. Small and simple vessel perforation plates evident across a growth ring (between arrows).

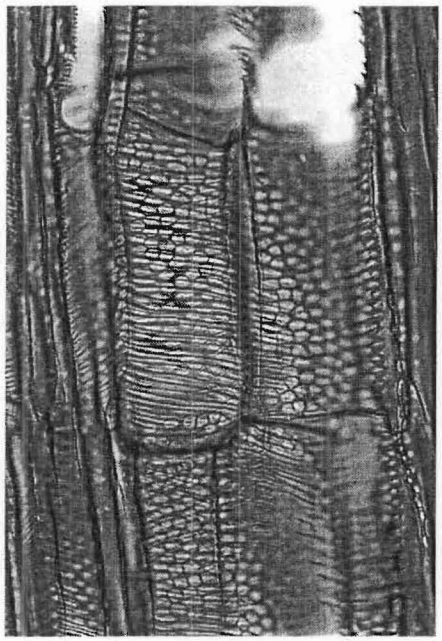
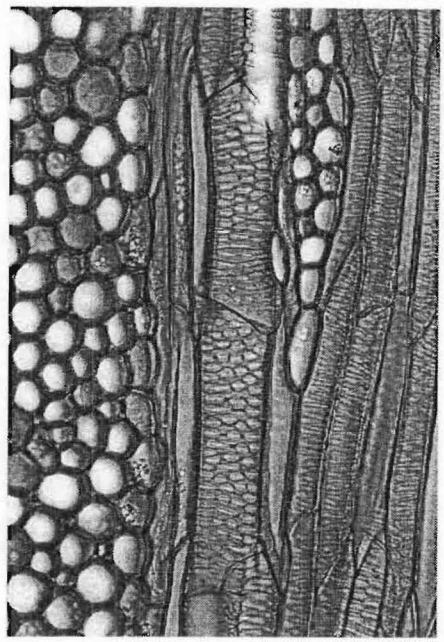


Figure 4.17



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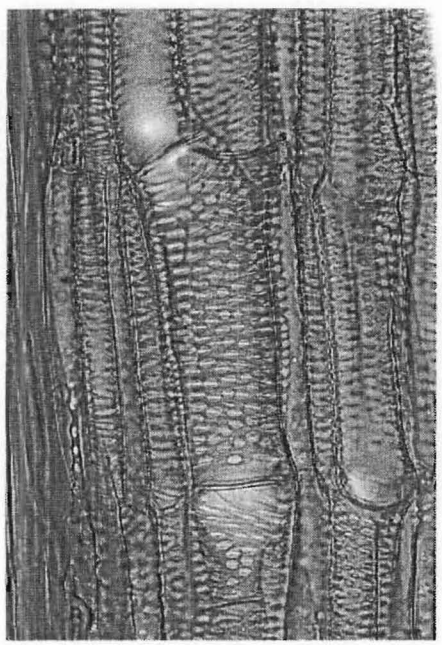

Figure 4.19

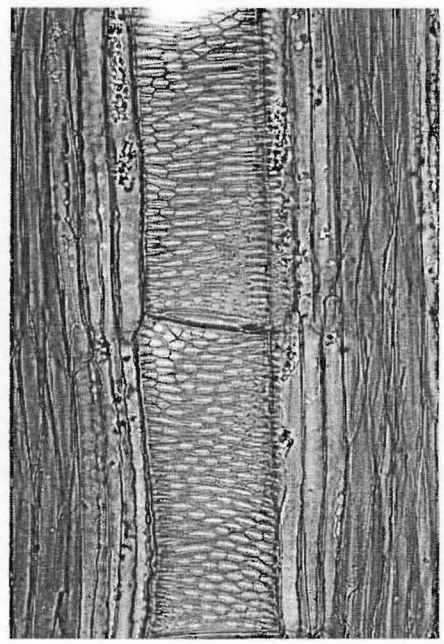

Figure 4.20

Fig. 4.17 *N. torulosum*. RLS ×320. Intervessel pits crowded, alternate, and polygonal in outline. Note helical thickenings. **Fig. 4.18** *Co. crassicaule*. TLS ×320. Intervessel pits crowded, alternate, polygonal in outline, and some pits elongated. Note helical thickenings. **Fig. 4.19** *Ca. williamsii*. RLS ×320. Intervessel pits slightly less crowded than Fig. 4.17 and 4.18. **Fig. 4.20** *Ca. odorata*. RLS ×250. Intervessel pits alternate, and elongated and sometimes opposite.

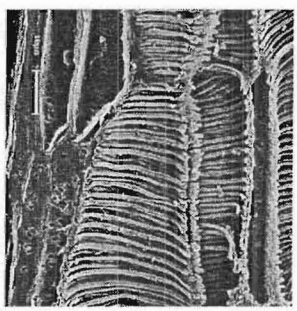

Figure 4.21

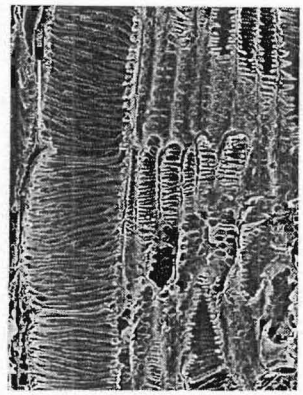

Figure 4.22

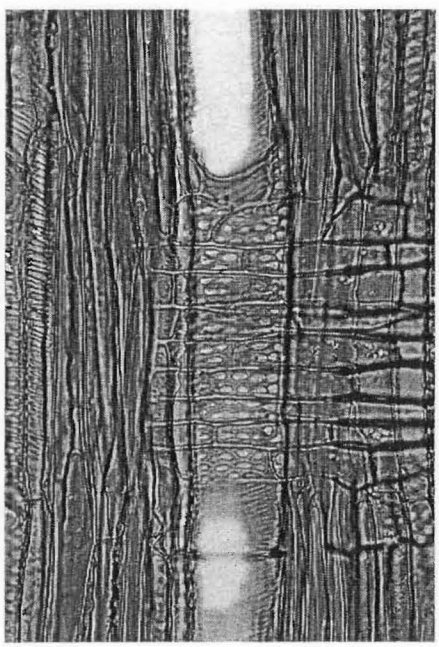

Figure 4.23

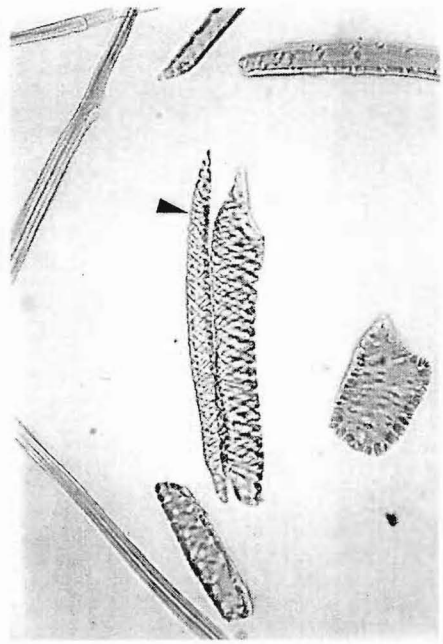

Figure 4.24

Fig. 4.21 *Ch. muritai*. SEM ×250. Helical thickenings on vessel elements. **Fig. 4.22** *Ca. nana*. SEM ×250. Wide diameter vessels with broad helical thickenings, and narrow diameter vessels with slender helical thickenings. **Fig. 4.23** *Ca. compacta*. RLS ×320. Vessel to ray pits. **Fig. 4.24** *Ca. compacta*. Maceration ×320. Vasicentric tracheid (arrow) associated with a wide vessel element.

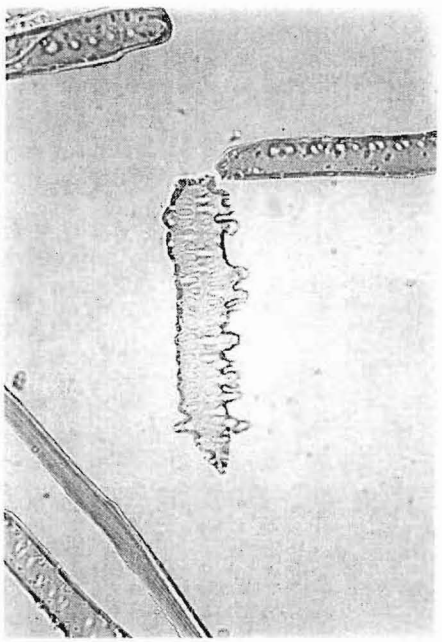

Figure 4.25

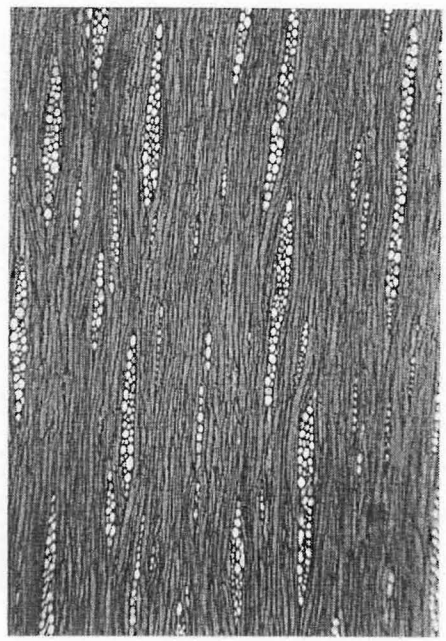

Figure 4.26

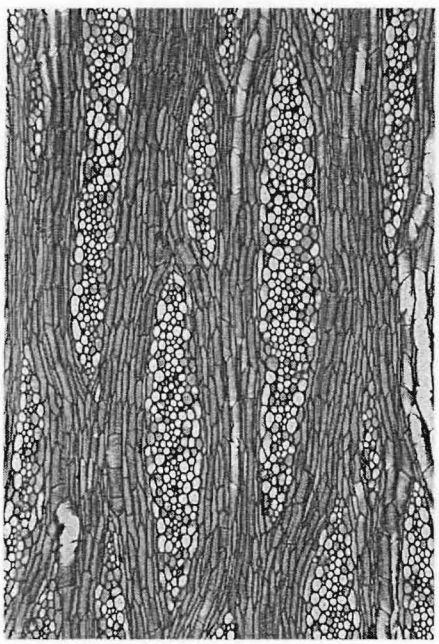

Figure 4.27

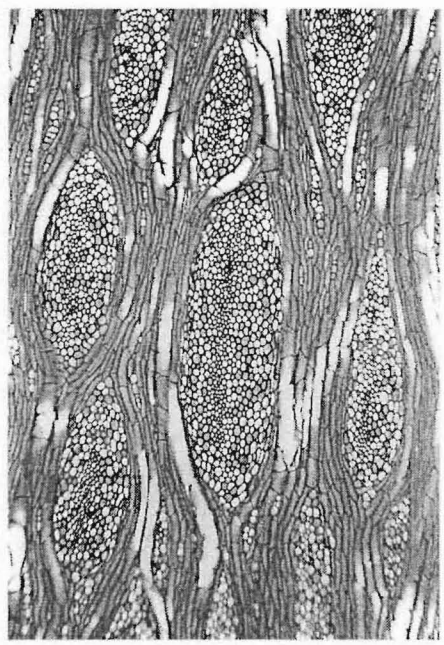

Figure 4.28

Fig. 4.25 *Ca. williamsii*. Maceration ×320. Fusiform parenchyma cell with disjunctive walls. **Fig. 4.26** *Ca. nana*. TLS ×80. Rays 1-4 cells wide. **Fig. 4.27** *Ca. nana*. TLS ×62. Rays 2-8 cells wide. Ray body cells with smaller diameter than ray margin cells. Note sheath cells and axial parenchyma with gable-ends. **Fig. 4.28** *Ca. nana*. TLS ×50. Rays 1-20 cells wide. Ray body cells with smaller diameter than ray margin cells. Note the storied structure is not clearly defined.

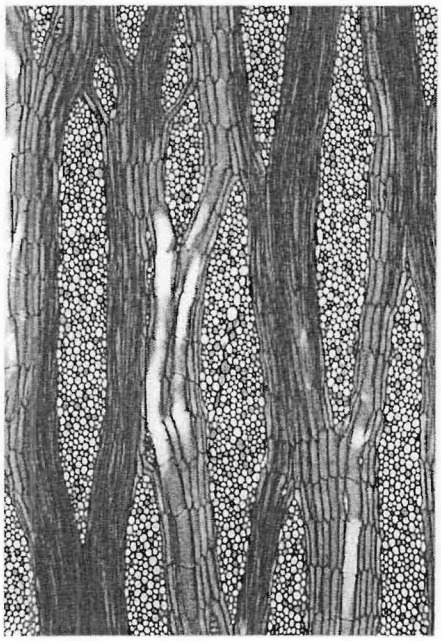

Figure 4.29

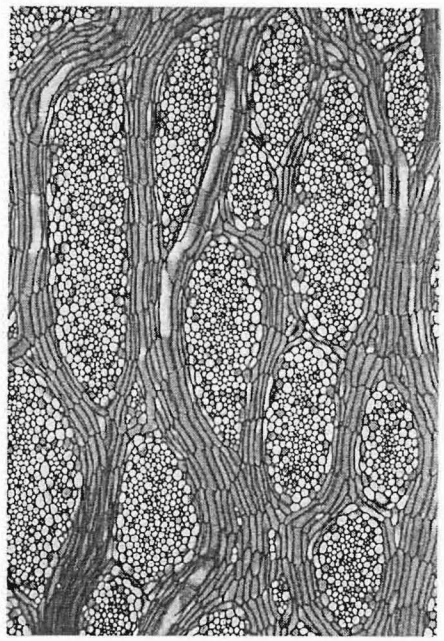

Figure 4.30

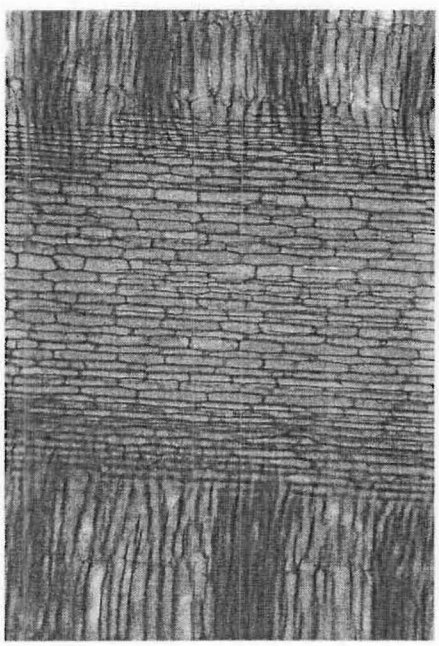

Figure 4.31

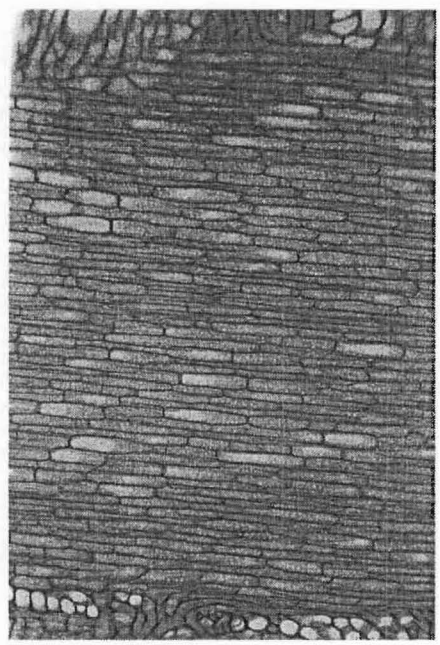

Figure 4.32

Fig. 4.29 *N. glabrescens.* TLS ×50. Rays 2-13 cells wide, and tall. Note the storied structure is clearly defined. **Fig. 4.30** *N. glabrescens.* TLS ×50. Rays 1-16 cells wide, and short. Note the storied structure is clearly defined. **Fig. 4.31** *Ch. stevensonii.* RLS ×80. Ray cells procumbent. Note the marginal cells with a smaller diameter than the body cells. **Fig. 4.32** *N. torulosum.* RLS ×80. Ray cells procumbent.

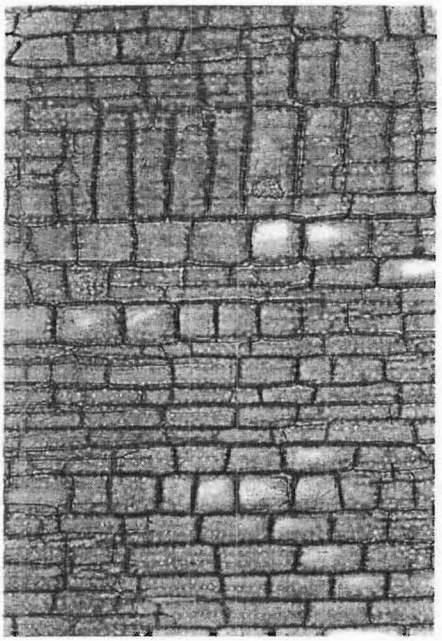

Figure 4.33

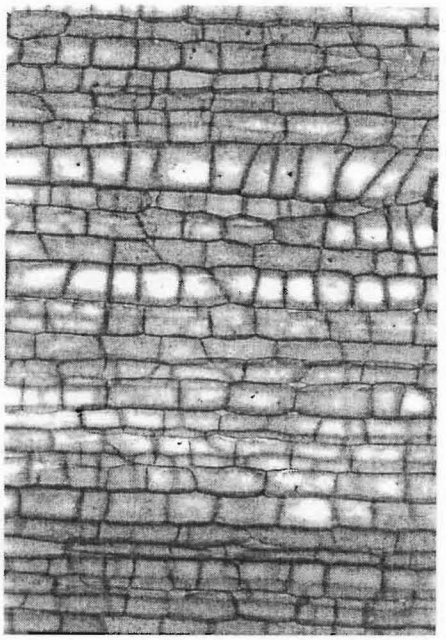

Figure 4.34

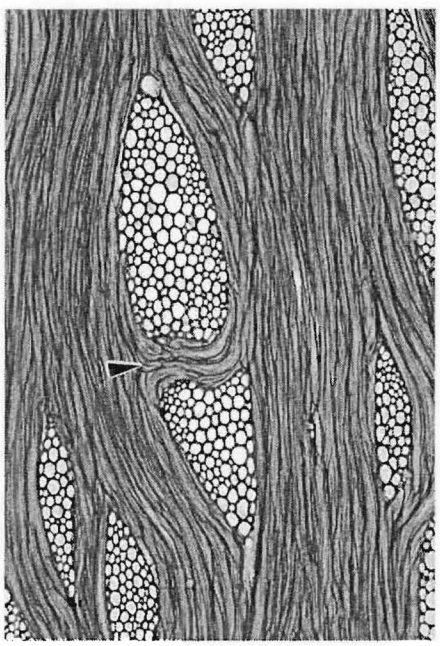

Figure 4.35

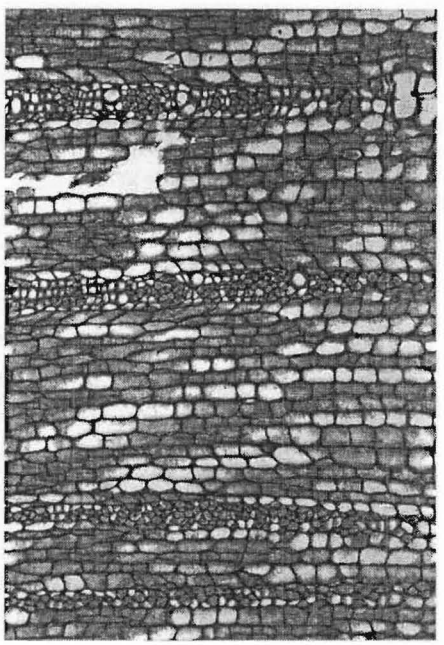

Figure 4.36

Fig. 4.33 *Ca. williamsii*. RLS ×156. Ray cells procumbent, square, and upright. **Fig. 4.34** *Co. crassicaule*. RLS ×200. Ray cells procumbent, square, and upright. **Fig. 4.35** *N. glabrescens*. TLS ×100. Ray dissected by fibres (arrow). **Fig. 4.36** *Ca. corrugata*. RLS ×80. Ray dissected by fibres in four places. Note also the procumbent, square, and upright cells.

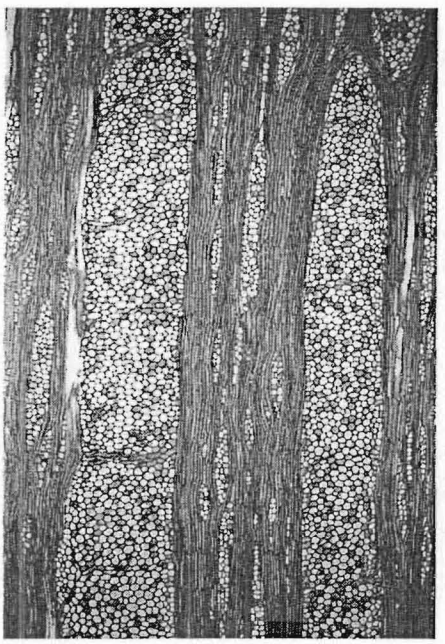

Figure 4.37

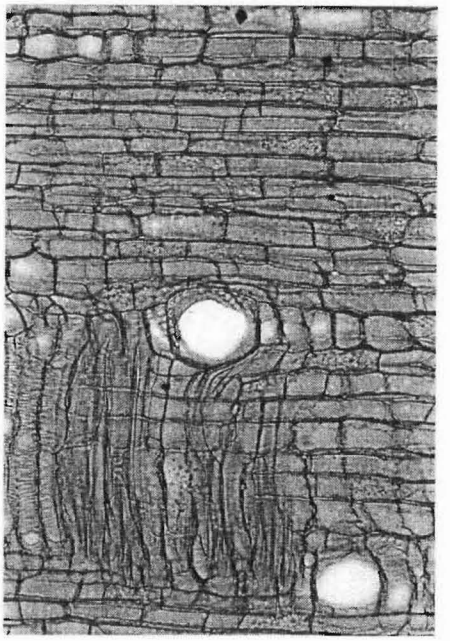

Figure 4.38

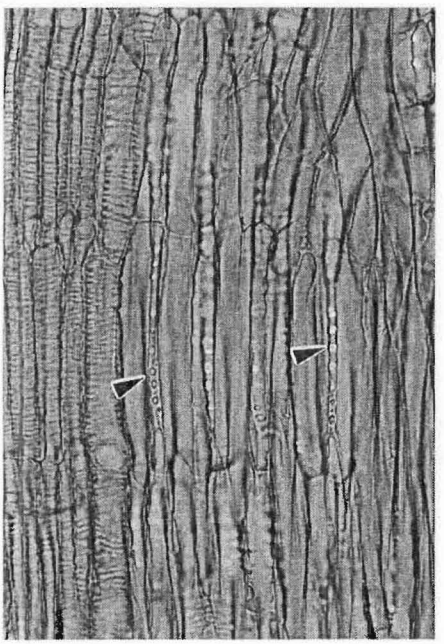

Figure 4.39

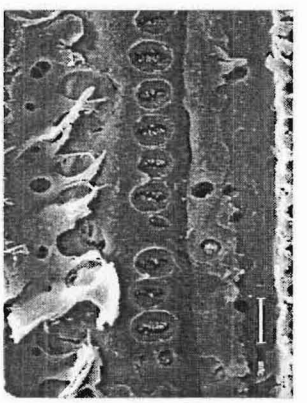

Figure 4.40

Fig. 4.37 *Ca. corrugata*. TLS ×31. Rays of two distinct sizes: 1-4 cells wide, and 12-16 cells wide. **Fig. 4.38** *Ca. compacta*. RLS ×200. Ray with simple perforation (arrow). **Fig. 4.39** *Ca. nana*. RLS ×320. Fibre tracheid (arrows). **Fig. 4.40** *Ca. nana*. SEM ×1200. Fibre tracheid with bordered pits and vestures.

CHAPTER FIVE

HETEROBLASTY

5.1 INTRODUCTION

A notable feature of the New Zealand flora is the large number of species that exhibit heteroblastic development. Cockayne (1928) estimated that New Zealand has about 200 such species, and about 165 of these have a prolonged juvenile phase. Notable examples of a pronounced juvenile-to-adult transition are *Pennantia corymbosa* and *Elaeocarpus hookerianus*.

In his paper on the seedlings of indigenous New Zealand plants Cockayne (1899) reported that the leafless species of *Carmichaelia* exhibit three stages of development: "first, a wiry or thick–stemmed seedling with compound leaves; second, leafy cladodes arising from the axils of the primary leaves; and third, quite leafless cladodes, often extremely thick and stout." Cockayne (1899, 1900) described the seedling form of *Carmichaelia angustata*[1], *C. enysii*, *C. hookeri*, *C. kirkii*, *C. odorata*, *Corallospartium crassicaule*, and *Notospartium torulosum*. Later, Cockayne (1912) referred to the leafy phase of *Carmichaelia*, *Notospartium*, and *Corallospartium* as a mesophytic juvenile, and to the leafless stage as a xerophytic adult.

Goebel (1900) introduced the terms `heteroblastic development' and `homoblastic development' in recognition of different forms of development. Heteroblasty occurs when the differences between juvenile and adult forms are great, while homoblasty refers to differences which "are very slight and the two sections [juvenile and adult] may quite gradually pass from one to the other" (Goebel 1900). An example of each feature was taken from *Carmichaelia*: development in seedlings of *Carmichaelia stricta* was described as heteroblastic, and that in *C. enysii* as homoblastic (Goebel 1900). Philipson (1964) has made an important distinction in dividing heteroblastic development into two groups: habit-heteroblasty occurs when there is "an abrupt break

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[1] Nomenclature for *Carmichaelia* follows the revision in Chapter 3, except when species names are cited from the works of earlier authors.

in the development of the habit of the plant", and leaf-heteroblasty refers to changes in leaf characters. Goebel's definition of homoblastic development inferred that there are slight differences between juvenile and adult forms. I prefer a more precise definition of homoblasty as when juvenile and adult growth habit, stems, and leaves are alike or similar.

Godley (1985) studied the seedlings, juveniles, and adults of a large number of New Zealand plants, and recognised 10 leaf and 4 branch classes which are associated with juvenile and adult growth forms. In his classification *Carmichaelia* is affiliated with *Phyllocladus alpinus*, as the leaves of both species are reduced to scales which are associated with cladodes.

This chapter describes the transition from juvenile to adult in 19 species of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. It further refines the seedling stages described by Cockayne (1899, 1900), and expands on Goebel's (1900) observation of heteroblasty and homoblasty in *Carmichaelia*. The discussion also considers the functional aspect of heteroblasty in terms of evolutionary ecology: how does variation in heteroblasty relate to the plants environment? The data on heteroblasty will be included in the phylogenetic analysis.

5.2 MATERIALS AND METHODS

Plants have been raised at the Landcare Research experimental plant nursery, Lincoln, from seed collected in the wild. Before sowing seeds were either soaked in hot water for 24 hours or physically scarified by chipping the seed coat with a scalpel. The seeds were sown on a peat and perlite seed-raising medium (1:1), covered in gravel chip, and placed in an unheated glasshouse. Germination usually occurred within 1-3 weeks. Plants were potted into a bark-based mix and grown in an unheated glasshouse. Weekly observations were recorded for stem and leaf characteristics. Where possible the experimental observations have been verified on wild plants.

The following species were studied: *Carmichaelia arborea*, *C. astonii*, *C. australis*, *C. compacta*, *C. corrugata*, *C. hollowayi*, *C. kirkii*, *C. monroi*, *C. nana*, *C. odorata*, *C. petriei*, *C. uniflora*, *C. williamsii*, *Chordospartium muritai*, *C. stevensonii*, *Corallospartium crassicaule*, *Notospartium carmichaeliae*, *N. glabrescens*, and *N. torulosum*. Herbarium vouchers have been deposited at CHR.

5.3 HABIT-HETEROBLASTY

Most species of *Carmichaelia* exhibit habit-heteroblasty, juvenile stems being flat, usually non-branching, decumbent, or occasionally weakly ascending (Table 5.1). In many species the adult stems are usually leafless, generally stouter, and differ in colour from juvenile stems. Adult stems usually emerge from just above the cotyledons or at the base of the juvenile stems in the first year after germination. The juvenile phase of *C. arborea*, for example, is characterised by thin, flat, brown-green, and decumbent stems up to 12 cm long, and the adult phase by stout, terete or subterete, green, and ascending stems (Fig. 5.1). Stems intermediate between adult and juvenile stems have not been observed. However, in *C. arborea* and the closely related *C. odorata* the adult stems are often leafy, and this lessens the contrast between the juvenile and adult phases. Other species have distinct juvenile and adult forms. In the rhizomatous *C. corrugata* (Fig. 5.2) the juvenile stems are up to 255 mm long, flaccid, decumbent or prostrate, rarely branched, brown, hairy, with up to 50 leaf nodes, and they bear 1(-3)-foliolate leaves. In contrast, the adult stems are up to 70 mm long, stiff, erect or spreading, regularly branched, orange-green, glabrous, with 2-12 leaf nodes, and they are leafless. The earliest adult shoots of *C. corrugata* arise just above the cotyledons, at the base of juvenile stems, or on the lower half of other adult stems. *Carmichaelia corrugata* initially forms a compact mound of erect adult stems, but at about 18 months rhizomatous stems emerge at the base of the reduced woody trunk. In at least one species, *C. compacta*, the adult stems often emerge from the growing tip of the juvenile stems (Fig. 5.3).

The dwarf-shrubby *C. astonii*, *C. monroi*, and *C. nana* and the shrubby *C. williamsii* lack the distinctive decumbent juvenile stems characteristic of the other species of *Carmichaelia* (Table 5.1). These species are homoblastic, exhibiting no change between the juvenile and adult stages. In *C. nana* the first cladodes to emerge from the axils of the cotyledons are erect or spreading, the lower nodes of a cladode have a few, small, unifoliolate leaves, and the upper nodes have scales. The plant quickly develops a well branched structure of leafless adult stems (Fig. 5.4). A single, erect, more-or-less leafless cladode of a young *C. nana* was illustrated as *C. enysii* by Cockayne (1900).

The juvenile stage of *Chordospartium muritai*, *C. stevensonii*, *Corallospartium*

Table 5.1 Leaf and stem characteristics of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*: ✓ present; - absent.

	Habit-heteroblasty	Orientation of juvenile stems	Leaf-heteroblasty	Leaflet number
Ca. astonii	-	erect	-	1
Ca. monroi	-	erect	-	1
Ca. nana	-	erect	-	1
Ca. williamsii	-	erect	-	1-5
Ca. arborea	✓	decumbent	-	1-5
Ca. australis	✓	decumbent	-	1-5
Ca. compacta	✓	decumbent	-	1-9
Ca. corrugata	✓	decumbent	-	1(-3)
Ca. hollowayi	✓	decumbent	-	1-3
Ca. kirkii	✓	decumbent	-	1-5
Ca. odorata	✓	decumbent	-	1-7
Ca. petriei	✓	decumbent	-	1-5
Ca. uniflora	✓	decumbent	-	1(-3)
Ch. muritai	✓	erect	✓	1
Ch. stevensonii	✓	erect	✓	1
Co. crassicaule	✓	erect	✓	1(-3)
N. carmichaeliae	✓	erect	✓	1
N. glabrescens	✓	erect	✓	1
N. torulosum	✓	decumbent	✓	1

crassicaule, *Notospartium carmichaeliae*, and *N. glabrescens* is characterised by erect or ascending, thin, flat, and leafy juvenile stems up to 18 cm tall (Table 5.1). In *N. torulosum*, however, the juvenile stems are decumbent or only weakly ascending, and the erect adult stems emerge from just above the cotyledons (Fig. 5.5). The adult stems of *Notospartium*, like those of all species of *Carmichaelia* studied, assume their fully developed adult form at the abrupt transition from juvenile to adult. In contrast, when the adult stems of *Chordospartium* and *Corallospartium* emerge they are not in their final form, and the development of the adult phase continues for a short period. This process is well illustrated by *Chordospartium stevensonii* (Fig. 5.6): the first one or two tiers of adult stems are light brown or yellow-brown and erect, the following one or two tiers of stems are brown-green and ascending or weakly spreading, and subsequent stems are greener and droop more noticeably as they become progressively more like mature adult stems. In *Corallospartium crassicaule* and *Chordospartium muritai* the juvenile stems are leafy, flat, erect, and moderately hairy, the first adult stems are leafless, subterete and densely hairy over the whole surface, and as the adult phase develops they become progressively stouter and the hairs are restricted to grooves in the stem.

5.4 LEAF-HETEROBLASTY

The leaves on juvenile and adult plants of all species of *Carmichaelia* are similar in size, shape, and colour (Table 5.1). The leaves can be brown, brown-green, or green, are sometimes mottled, and are either hairy or glabrous. Obovate or oblanceolate unifoliolate leaves occur on the dwarf shrubby *C. astonii*, *C. hollowayi*, *C. monroi*, *C. nana*, and *C. vexillata*. In *C. hollowayi*, *C. corrugata*, and *C. uniflora* the leaves of juvenile and adult plants are usually unifoliolate on wild and most cultivated plants, but sometimes vigorously growing cultivated plants produce bifoliolate or trifoliolate leaves (Fig. 5.7). The remaining species of *Carmichaelia* initially have a few unifoliolate leaves which are followed by a series of compound leaves in which the number of leaflets progressively increases. The leaves of *C. compacta* and *C. odorata* have up to nine and seven leaflets, respectively, whereas *C. appressa*, *C. arborea*, *C. australis*, *C. curta*, *C. juncea*, *C. kirkii*, *C. petriei*, and *C. williamsii* generally have up to five leaflets. In *Carmichaelia* the leafiness of the juvenile phase varies between the compound and

abundantly leafy *C. compacta* (Fig. 5.3), and the unifoliolate and sparsely leafy *C. nana* (Fig. 5.4). Leafiness of individual adult *Carmichaelia* plants varies considerably in the field: for example, *C. arborea* and *C. odorata* are usually leafy, but sometimes leafless; *C. australis*, *C. hollowayi*, *C. kirkii*, *C. petriei*, and *C. vexillata* are usually leafless, but occasionally with a few leaves; and *C. compacta*, *C. curta*, *C. monroi*, and *C. nana* are almost always leafless. In *Carmichaelia*, when leaves are absent, the stipules are fused together to form a scale (Slade 1952, fig. 1). The change from leaves to scales occurs gradually, with leaflet size decreasing in both compound and unifoliolate leaves. In compound leaves the leaflet number also reduces.

In *Chordospartium*, *Corallospartium*, and *Notospartium* the leaves are obcordate or orbicular in the juvenile and elliptic in the adult (Fig. 5.7; Table 5.1). In both juvenile and adult stages the leaves are green, usually with a glabrous and dull lamina, and often with a fringe of hairs on the margin. *Chordospartium* and *Notospartium* have exclusively unifoliolate leaves, whereas *Corallospartium* has predominantly unifoliolate leaves, but three of the seven seedlings studied each had 1-3 trifoliolate leaves. On adult plants of *Chordospartium*, *Corallospartium*, and *Notospartium* leaves are replaced by scales formed from fusion of the stipules. However, numerous elliptic leaves were induced on 3-year-old adult plants of *Chordospartium muritai*, *C. stevensonii*, and *Corallospartium crassicaule* by placing plants in partial shade and subjecting them to high humidity. Under these conditions a 3-year-old adult plant of *Notospartium glabrescens* produced only a few leaves.

5.5 DISCUSSION

The ecological significance of the leafy juvenile stage reported here for *Chordospartium*, *Corallospartium*, *Notospartium*, and most species of *Carmichaelia* is likely to be related to successful post-germination establishment. During the establishment phase it would be advantageous for plants to have leaves and photosynthetic juvenile stems. Once established, individual plants undergo a reduction in leaf size and number as they progress towards the xeromorphic condition. The leafless adult form usually develops during the first year after germination, and the juvenile and adult phases persist together for a period of time.

The variations in growth habit reported here can be correlated with habitat

preferences. *Notospartium torulosum* and most species of *Carmichaelia* are more suited to open situations as they have decumbent juvenile stems. Species of *Carmichaelia* commonly colonise open habitats such as sparsely vegetated rock outcrops, newly exposed surfaces, and the margins of forest, scrub, and dense grassland. For example, *C. odorata* frequently colonises newly deposited landslips and glacial moraine on the West Coast of the South Island; *C. australis* seedlings can be found among low-growing herbs and grasses in the Canterbury foothills; and *C. corrugata* occurs on river gravels and sparsely vegetated terraces. *Notospartium torulosum* (Fig. 5.5) is probably suited to growing on and around the margin of rock outcrops. In original and undisturbed conifer-hardwood forest near Mt Peel, South Canterbury, somewhat sprawling and decumbent adult plants of *N. torulosum* are common on sparsely vegetated rock outcrops (B. P. J. Molloy pers. comm.). In areas where the original forest cover has been burned or cleared, including places near Mt Peel, *N. torulosum* occurs as erect shrubs in secondary scrub or tussock-grassland.

The erect juvenile stems of *Chordospartium*, *Corallospartium*, *Notospartium carmichaeliae*, and *N. glabrescens* correlate well with shaded forest margins and tall scrub habitats. *Chordospartium stevensonii*, *N. carmichaeliae*, and *N. glabrescens* occur in Marlborough and are riparian species often associated with forest margins and tall scrub of *Olearia paniculata* and *Kunzea ericoides*. The habitat of *Corallospartium* is problematic as its distribution in upland regions of the South Island coincides with vegetation which has been highly modified by burning or clearing. *Corallospartium* is now found in a variety of habitats including rock outcrops, tussock grassland, and montane scrub. However, the erect juvenile stems suggest that it is adapted to shaded forest margins and dense montane scrub communities.

Carmichaelia astonii, *C. monroi*, and *C. nana* lack an obvious mesomorphic juvenile stage, and these species usually occur on dry and open sites, including river gravels and terraces, outwash fans, or loose and rubbly rock or limestone outcrops. This open habitat may have favoured the evolution of the virtually leafless xeromorphic juvenile form, and acted against the need for a leafy juvenile phase which would find growing conditions difficult in dry and exposed situations.

The leaf, stem, and growth habit features described are shared in different combinations among *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* (Table 5.1). This variation raises several questions about character

evolution and the circumscription of the four genera. The characters described here will be included with a larger set of morphological and anatomical characters in a cladistic analysis.

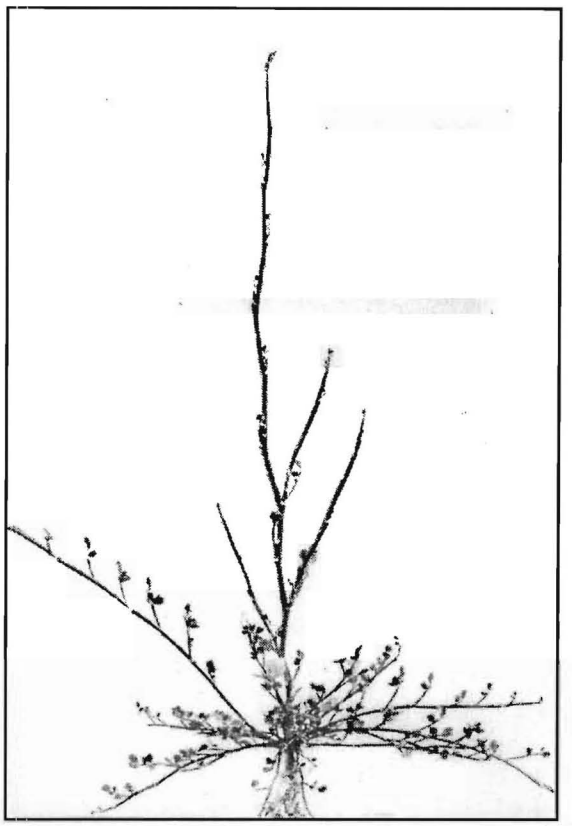

Fig. 5.1 *Carmichaelia arborea* with decumbent and leafy juvenile stems and ascending, more-or-less leafless adult stems (1 year old).

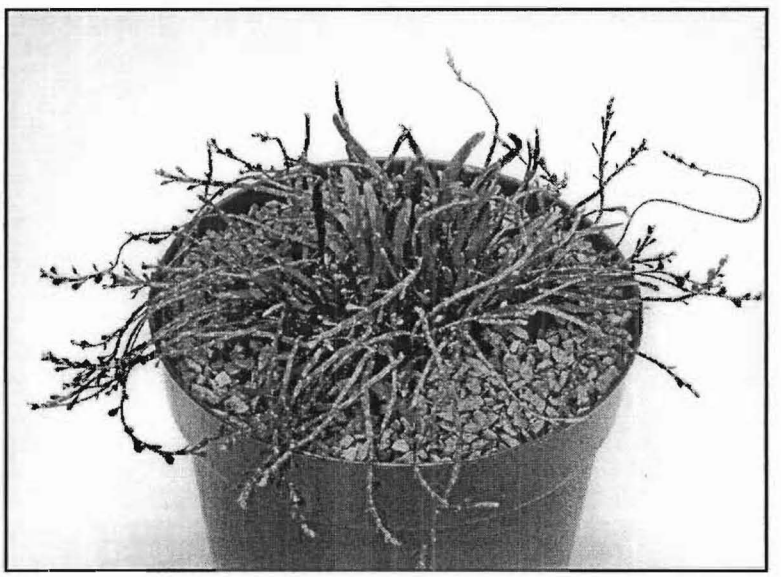

Fig. 5.2 *Carmichaelia corrugata* with numerous long, decumbent, and leafy juvenile stems and short, erect, leafless adult cladodes (2 years old).

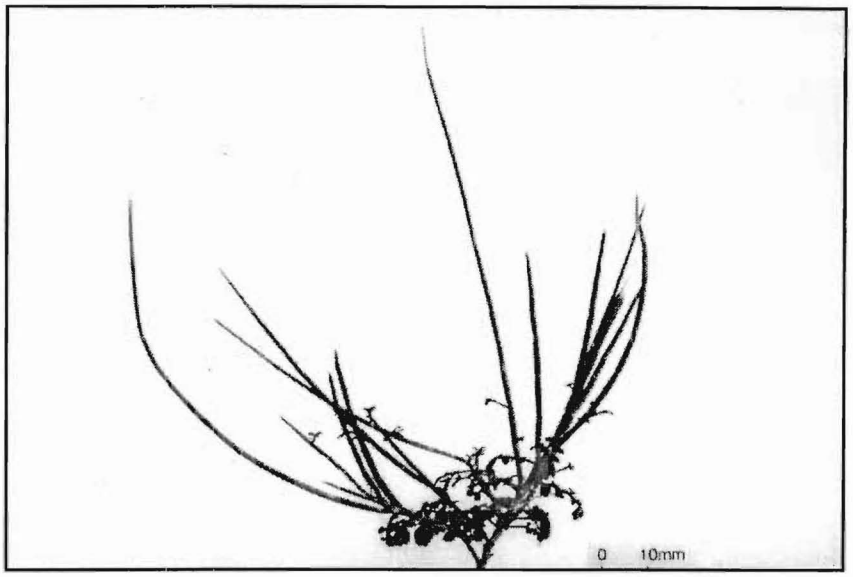

Fig. 5.3 *Carmichaelia compacta* with many juvenile compound leaves and leafless adult stems (1 year old).

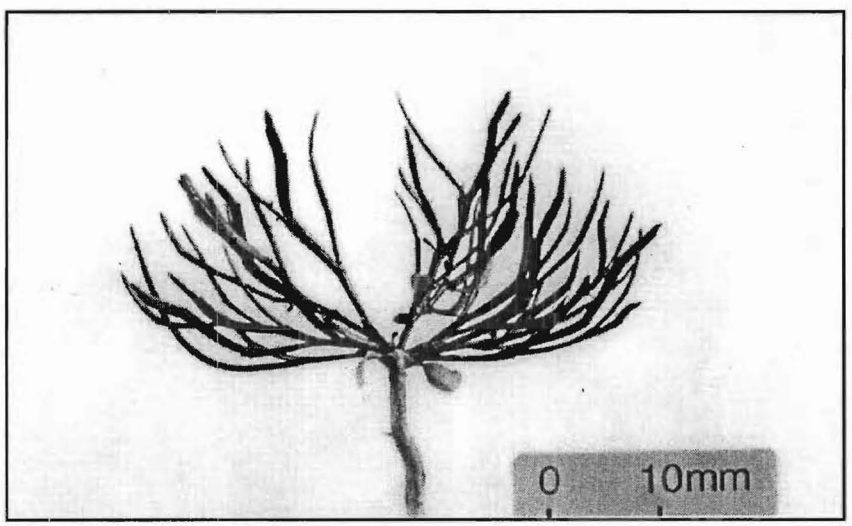

Fig. 5.4 *Carmichaelia nana* lacking an obvious juvenile phase and with very few unifoliolate leaves (8 months old).

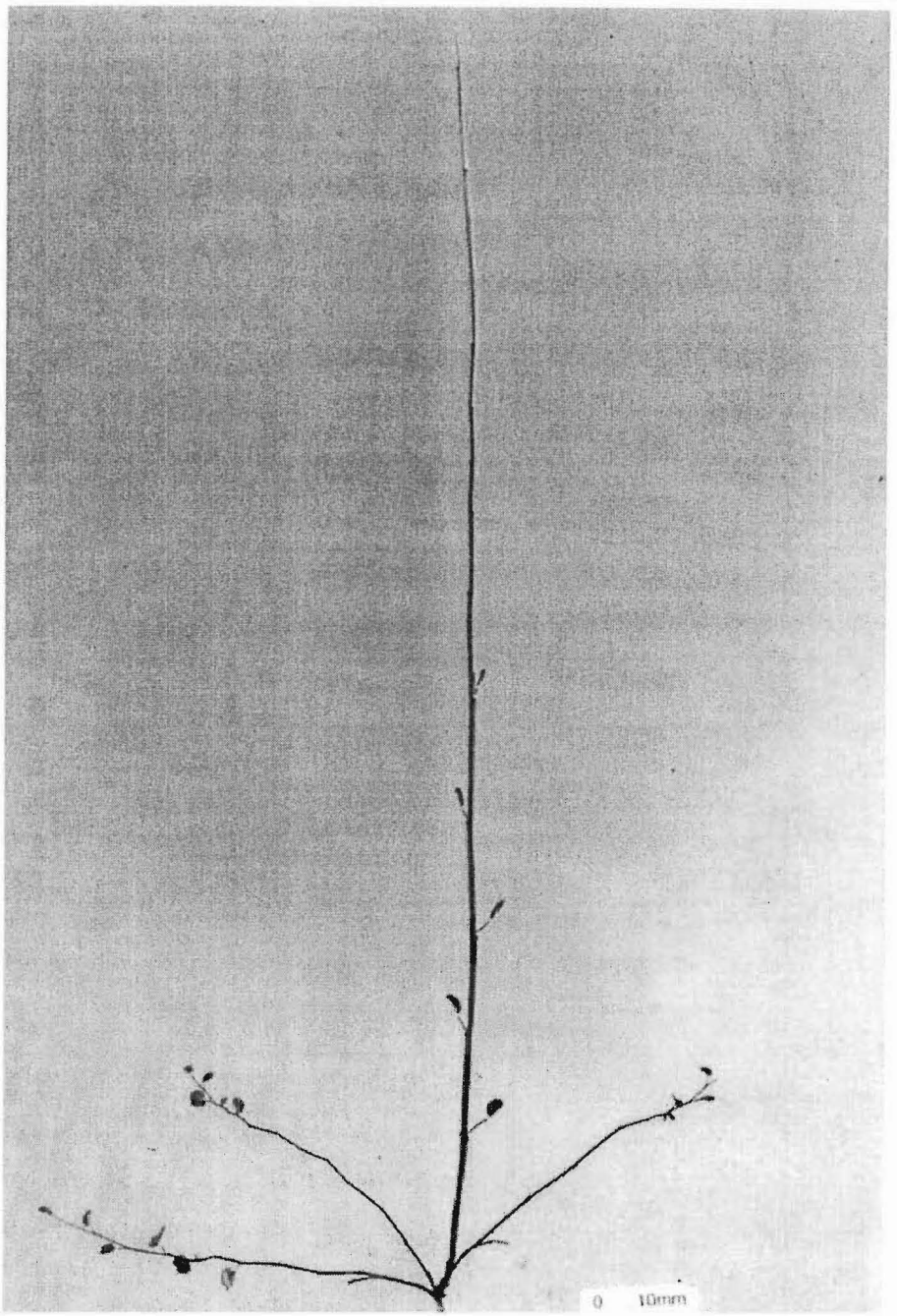

Fig. 5.5 *Notospartium torulosum* with decumbent or spreading juvenile stems and a single erect adult stem (1 year old).

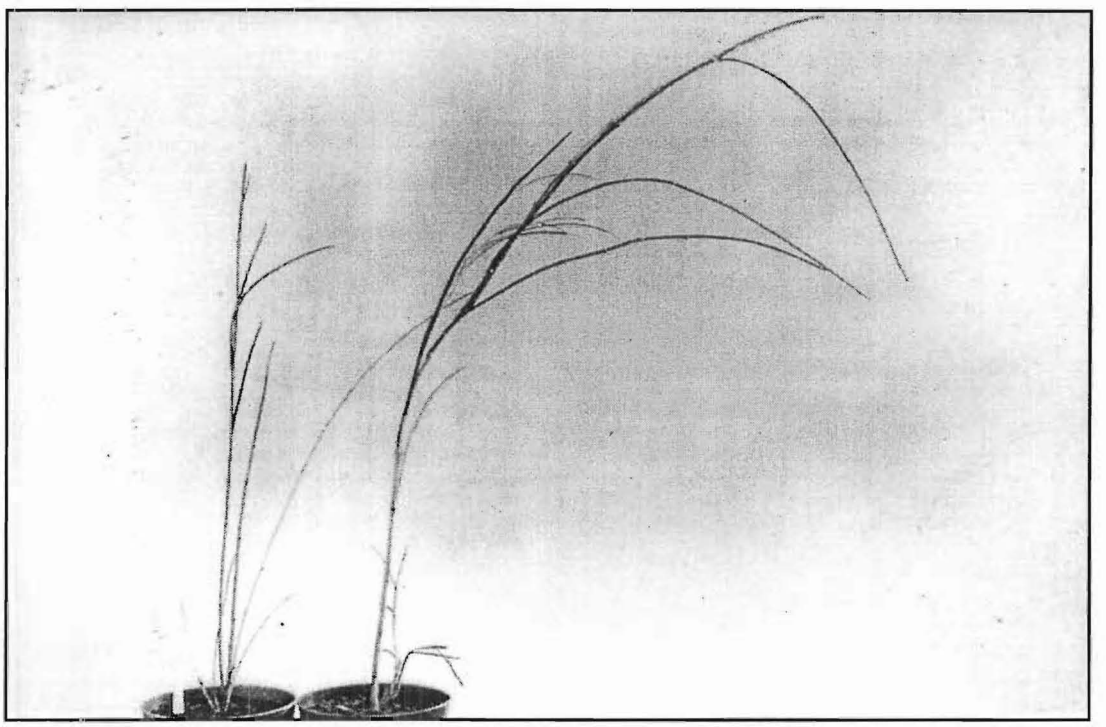

Fig. 5.6 *Chordospartium stevensonii*: left, 1 year old plant with several erect adult stems; right, 2 year old plant with adult stems becoming increasingly greener and pendulous, and short and now leafless juvenile strems at the base.

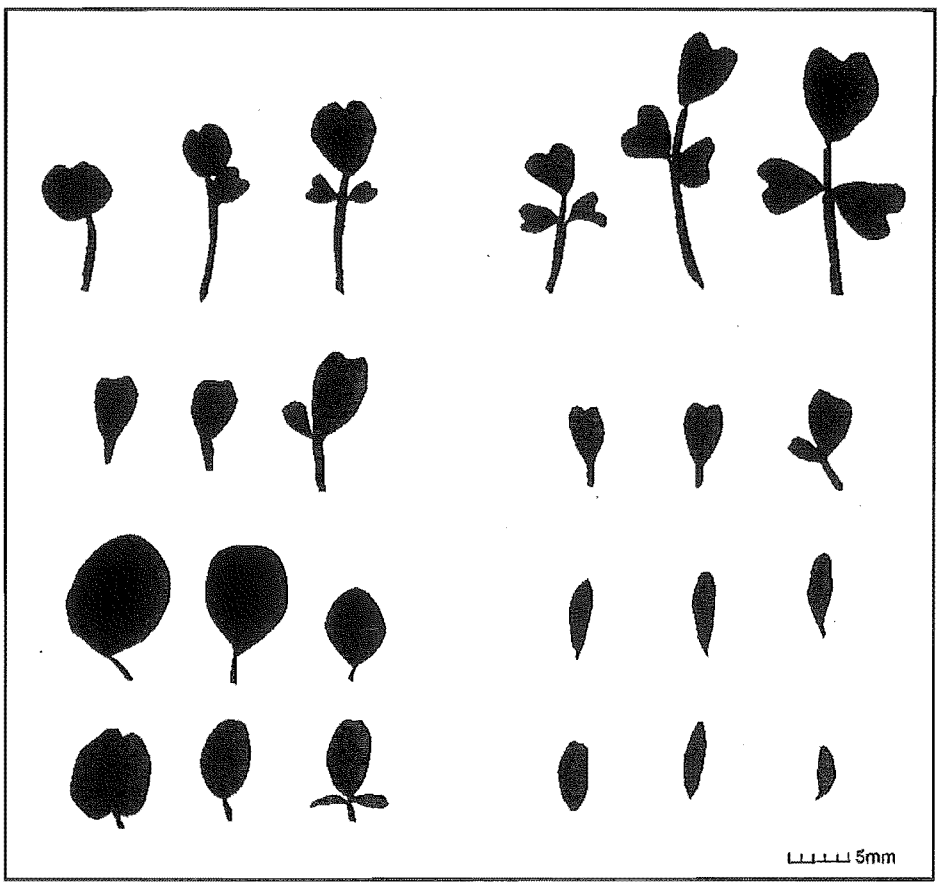

Fig. 5.7 Leaves. A, *Carmichaelia arborea*; B, *Carmichaelia hollowayi*; C, *Notospartium glabrescens*; D, *Corallospartium crassicaule*. Left, three leaves from a juvenile plant; right, three leaves from an adult plant. Leaves of *C. hollowayi* from the same plant, leaves of the other speciews from different plants.

CHAPTER SIX

PHYLOGENETIC ANALYSIS

6.1 INTRODUCTION

The first part of the process in constructing an evolutionary taxonomy classification is to undertake a phylogenetic analysis. This provides a hypothesis for an evolutionary history of the group, indicates relationships among taxa, and facilitates an analysis of character evolution, distribution, and divergence. The development of a phylogenetic hypothesis for an evolutionary classification is in agreement with phylogenetic systematics (e.g., Mayr 1981, 1988), and therefore to generate the phylogenetic hypothesis it is appropriate to use phylogenetic methods (Wiley 1981; Humphries & Funk 1984; Janvier 1984; Funk & Brooks 1990). Using methods of phylogenetic analysis does not imply that cladistic principles are being applied. The phylogenetic analysis presented here is based on evolutionary taxonomy and includes characters that are autapomophic and continuous. These types of characters are usually excluded by strict adherents to the principles of cladistics.

A phylogenetic analysis includes three main steps (Humphries & Funk 1984), although Stuessy (1980) has identified eight steps. The procedure outlined by these authors is summarised below under three main headings.

The sampling of taxa and the choice of characters. The study group (ingroup) is selected and the probable sister groups and outgroups determined. Characters of evolutionary interest are selected, and their states determined. Care is taken to select characters that occur in the ingroup and outgroup, those that have discrete states, and those with high levels of conservatism and low levels of variation.

Quantitative characters are generally not used for a phylogenetic analysis (Pimentel & Riggins 1987; Farris 1990), but can be if they are scored into discrete categories (Baum 1988; Sanderson 1989a; Strait et al. 1996). An argument against their use is that because of their continuous nature and the artificial methods used to categorise them, they offer little phylogenetic information. However, this *a priori* excludes the possibility that continuous characters could be phylogenetically informative.

The determination of synapomorphies. Characters are judged to be homologous, and the evolutionary direction of the states determined (i.e., primitive v's derived). Three criteria are available for the identification of homologies; common is primative, ontogeny, and outgroup comparison. The most useful operational method is outgroup comparison (Watrous & Wheeler 1981), where for a given character with two or more states within a group, the state occurring in the outgroup is assumed to be the ancestral state. This method usually examines characters of the ingroup, the immediate sister taxa to the ingroup, and another taxon that is sister group to the ingroup and immediate sister group; the closely and distantly related sister taxa form the outgroup (Stevens 1980). To select the outgroup it is possible to rely on other studies that have identified a sister group or higher level taxonomic relationships. When characters and their states have been defined and data gathered a data matrix of taxa and characters is constructed.

A search for the most parsimonious cladogram. The most parsimonious cladogram is that in which the character distribution requires the smallest number of postulated events of parallel or convergent evolution. Parsimony avoids as much as possible multiple origins for homologous features, provides the most robust phylogenetic hypothesis, and that with the greatest explanatory power. HENNIG86 (Farris 1988) and PAUP (Swofford 1993) are two of the main programmes used for phylogenetic analysis of morphological data. A limitation of HENNIG86 is that it allows only binary characters to be analysed. PAUP is the most powerful programme as it offers many different options for data analysis. These include contraints on permissible character changes: Wagner parsimony allows free irreversibility of binary or ordered multistate characters; Fitch parsimony allows multistate characters to be unordered; Dollo parsimony permits each derived character state to originate only once. Characters may also be weighted by different values, and character transformation can be accelerated (ACCTRAN) or delayed (DELTRAN). Accelerated transformation will lead to a single origin for a character followed by a reversal, whereas delayed transformation will lead to a preference for two independent origins.

The search for the most parsimonious set of trees is based on exact or heuristic methods (Swofford 1993). Exact methods guarantee to find all the most parsimonious trees in data sets of about 10 or fewer taxa, whereas heuristic methods will not find all trees in a large data set but require far less computer time. Heuristic methods select an

initial tree (or set of trees) by stepwise addition, then by branch swapping the tree is subjected to trial rearrangements to find shorter trees. Stepwise addition has four options for the addition of taxa to the analysis. These are "as is", "closest", "simple", and "random". The random addition sequence is the most thorough method to identify the most parsimonious trees. Several replicates of the random addition sequence can be used to evaluate the effectiveness of the heuristic search; if the same set of trees are found under each random search it is reasonable to assume all of the most parsimonious trees have been found.

The thoroughness of the search can be further enhanced by the STEEPEST DESCENT option. When this option is on the search continues branch swapping on all trees of a particular length until all trees have been examined, even after a new shorter length tree has been found partway through the search.

At the end of a search there is usually a set of most parsimonious trees. These can be summarised into a single strict consensus tree which contains only those groups that occur in all of the most parsimonious trees. Another summary tree is the majority rule consensus tree which includes only those branches that occur in 50% of the most parsimonious set of trees.

Once the phylogenetic analysis has been completed the resulting trees can be examined by MacClade which is an interactive programme for exploring the phylogeny (Maddison & Maddison 1992). MacClade allows for character evolution to be examined and reconstructed, and where necessary to move branches, reroot clades, create polytomies, and automatically search for more parsimonious trees. As trees are altered MacClade updates statistics such as the number of steps for each character and treelength. MacClade is interactive with PAUP and has a data editor where systematic and comparative data are entered and edited.

The general introduction to the thesis (Chapter 1) implied that there are several contradictions between characters and the generic boundaries of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. These four genera are recognised by differences in pods, inflorescences, and growth habit but, as noted by Hooker (1864), Cheeseman (1911), and Slade (1952, 1953), their boundaries are rather arbitrary. A phylogenetic study was undertaken of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* to elucidate patterns of character evolution and species relationships, and to define more clearly the generic boundaries. In particular,

the following hypotheses were tested:

1. Is *Carmichaelia* monophyletic as currently circumscribed, or paraphyletic by the exclusion of *Chordospartium*, *Corallospartium*, and *Notospartium*?

2. Does *Carmichaelia* have monophyletic sections or subgenera? For example, are the sections *Eucarmichaelia*, *Nana* (Kirk 1899), and *Huttonella* (Cheeseman 1906), and Simpson's (1945) eight subgenera monophyletic?

6.2 MATERIALS AND METHODS

6.2.1 Terminal taxa

The ingroup includes from New Zealand 17 species of *Carmichaelia*, 3 species of *Notospartium*, 2 species of *Chordospartium* (Purdie 1985), *Corallospartium crassicaule*, *Clianthus puniceus*, and *Swainsona novae-zelandiae* (Appendix 4). From Australia are included *Ca. exsul* from Lord Howe Island, and 12 species of *Swainsona* which represent 11 of the 13 informal species-groups recognised by Thompson (1993). These species include *S. galegifolia* (group 1) the type species for *Swainsona*, *S. formosa* (group 3) which has only recently been transferred to *Swainsona* from *Clianthus* (Thompson 1990), and *S. lessertiifolia* and *S. microphylla* which were included by Thompson (1993) with *S. novae-zelandiae* in group 9.

Astragalus bisulcatus, *Biserrula pelecinus*, *Lessertia perennans*, and *Sutherlandia fruticosa* were selected as outgroup species (Appendix 4), and the tree was rooted by *Astragalus bisulcatus*. Four recently published molecular phylogenies enabled the outgroup taxa to be selected with some confidence. In analyses of chloroplast DNA Liston & Wheeler (1994) and Sanderson & Liston (1995) reported the following relationship: ((*Swainsona macculochiana*, *Clianthus puniceus*) *Sutherlandia frutescens*). This clade formed a trichotomy with *Lessertia annularis* and species of *Astragalus* and *Oxytropis*. A sister clade to this group was predominantly *Astragalus*, but also included *Biserrula pelecinus*. Sanderson & Liston (1995) also analysed the ITS region of the nuclear ribosomal DNA and in their consensus tree *Swainsona pterostylis* and *C. puniceus* were sister species, as were *Lessertia* and *Sutherlandia*, but these two groups were on different parts of a larger clade which also included *Colutea* and *Sphaerophysa*. Sanderson & Wojciechowski (1996) analysed a similar data set, but also included *Carmichaelia williamsii* which was sister species to *C. puniceus*.

Following the most recent classification of the Fabaceae subfamily Faboideae (Polhill 1981) several of the study species were included in the tribe Galegeae. The Galegeae subtribe Coluteinae is represented by *Clianthus*, *Swainsona*, *Sutherlandia*, and *Lessertia*, and subtribe Astragalinae by *Astragalus* and *Biserrula*. The tribe Carmichaelieae (Hutchinson 1964; Polhill 1981) is represented by *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*. *Sphaerophysa salsula* (Galegeae subtribe Coluteinae) and the extinct *Streblorrhiza speciosa* (tribe Carmichaelieae) were also considered for the data set as outgroup and ingroup taxa respectively, but a lack of available plant material prohibited their inclusion.

Historically, the tribal placement of the legume genera included in this study has been the subject of much conjecture, and this has been summarised by Sanderson & Liston (1995). However, on the basis of molecular, morphological, and cytological evidence Sanderson & Wojciechowski (1996) suggested that the tribe Carmichaelieae is closely allied to the Galegeae subtribe Coluteinae, and that it would be better united with that group to form what they called an "Astragalean clade." This "Astragalean clade" includes one branch dominated by *Astragalus* and another branch with *Clianthus*, *Swainsona*, and *Carmichaelia*. Differentiation along geographic lines for Australia, New Zealand, and South Africa was noted by Sanderson & Liston (1995). Liston & Schwarzbach (in Sanderson & Liston 1995) have indicated the occurrence of a monophyletic Australian and New Zealand clade including *Swainsona*, *Clianthus*, and *Carmichaelia*. Thus, the separation of the tribe Carmichaelieae from *Swainsona* and *Clianthus* of the Galegeae subtribe Coluteinae would appear to be unnatural, and not the best representation of evolutionary relationships. Because of these close relationships the *Carmichaelia* complex, *Clianthus*, and *Swainsona* are often referred to as galegoid legumes, and this, in a broad sense, invokes the tribe Galegeae sensu Bentham (Bentham & Hooker 1865).

6.2.2 Character selection and coding

The data matrix (Appendix 5) includes 47 characters, each of which was carefully selected to provide data that would support groups of species. To gain an indication of characters that had proven phylogenetically useful in the Fabaceae, other published studies were critically examined. In this regard, the most useful papers were those

published in *Advances in Legume Systematics Part 7 Phylogeny* (Crisp & Doyle 1995). The data for each character were usually taken from the taxonomic descriptions for *Carmichaelia* in Part I of the thesis, herbarium specimens (see Appendix 4), and/or the revision of Thompson (1993). Several of the characters are new and are reported in this thesis for the first time (e.g., those of wood anatomy, Chapter 4).

For several characters specific procedures to obtain the data were used. For example, to determine for all species whether vessels are with or without helical thickenings it was necessary to examine additional species to those reported in the wood anatomy study (Chapter 4). For these species a sample from a herbarium sheet (see appendix 4) was taken, macerated with hydrogen peroxide and glacial acetic acid (1:1), and examined under a light microscope. The presence or absence of helical thickenings is easily seen with a light microscope but was confirmed by SEM. To determine whether the phloem contains rigid or flexuose fibres (character 14) and if stone cells are present (character 15) a sample of bark from each species was macerated with hydrogen peroxide and glacial acetic acid (1:1). The fibres were examined and the presence or absence of stone determined with a light microscope.

Seven of the characters are anatomical, nine are vegetative (including growth habit), sixteen are taken from the inflorescence and flower, fourteen from the fruit and seed, and one is cytological. Characters were polarised by outgroup comparison (Maddison et al. 1984).

Five characters (11, 26, 31, 33, 44) are continuous quantitative and are scored by polymorphism overlap coding (Sanderson 1989a). In this coding method the traits are scored as multistate unordered characters coded 0-9, where the integers are scaled by the range of the character. The integer corresponding to the sample mean for the taxon was determined and then all integer states that occurred in the range of plus or minus one standard deviation were included in the data matrix as polymorphism. Although the use of quantitative characters for phylogenetic analyses is being debated (e.g., Farris 1990; Thiele 1993), they are included in this analysis as a range of measurements is often characteristic of a species, or group of species. Eight characters, including the five continuous quantitative characters, were scored only for the *Carmichaelia* complex because they were difficult to code for other taxa due to the limited number of available specimens or difficulties in character coding. In the data matrix (Appendix 5) missing data are coded as "?", and the states for polymorphic characters are enclosed within "{}"

brackets.

Characters and their states

1. Growth habit I. 0 = herbaceous; 1 = woody shrub; 2 = woody subshrub; 3 = woody liana. The New Zealand species are woody whereas all the other species are herbaceous or annual.

2. Growth habit II. 0 = not or only occasionally rhizomatous; 1 = strongly rhizomatous. A strongly rhizomatous growth habit is characteristic of *Ca. corrugata*, *Ca. uniflora*, and *S. novae-zelandiae*.

3. Habit-heteroblasty. 0 = absent; 1 = present: juvenile erect, adult gradual change; 2 = present: juvenile erect, adult no change; 3 = present: juvenile prostrate. Chapter 5 describes several patterns of heteroblastic development in the *Carmichaelia* complex which cut across the current generic boundaries. *Swainsona galegifolia* was grown from seed and this lacks heteroblasty.

4. Innovation shoots. 0 = basal; 1 = terminal. New vegetative shoots arise at terminal positions (*Carmichaelia* complex, *Clianthus*, *S. novae-zelandiae*, *Lessertia perennans*, *Sutherlandia frutescens*) or at the crown (Australian *Swainsona*, *Astragalus bisulcatus*, *Biserrula pelecinus*).

5. Leaf-heteroblasty. 0 = absent; 1 = present. The leaves of *Chordospartium*, *Corallospartium*, and *Notospartium* are a different shape in the juvenile and adult (see Chapter 5). Leaf-heteroblasty is absent in *Swainsona galegifolia* and *S. novae-zelandiae*.

6. Leaflet number. 0 = 12+; 1 = 2-11; 2 = unifoliolate. The subshrub species of *Carmichaelia*, *Notospartium*, and *Chordospartium* have unifoliolate leaves, whereas other species of *Carmichaelia*, *Clianthus*, and *Swainsona* have compound leaves. *Corallospartium*, *Ca. corrugata*, and *Ca. uniflora* usually have unifoliolate leaves, but sometimes bi- and trifoliolate leaves occur.

7. Leaves on adult plants. 0 = present; 1 = usually absent. Most adult plants of the *Carmichaelia* complex are leafless, or nearly so (see Chapters 3, 5). Adult plants of all the other species are leafy.

8. Stem pith. 0 = absent; 1 = present. Persistent pith is characteristic of the *Carmichaelia* complex, *Clianthus*, and *S. novae-zelandiae*, but the stems are hollow in the Australian species of *Swainsona* and the outgroup species.

9. Pith outline. 0 = round; 1 = compressed. Pith outline is round in the outgroup species, *Swainsona*, *Clianthus*, and *Ca. kirkii* (Slade 1952), but compressed in all other species of the *Carmichaelia* complex.

10. Vessel element helical thickenings. 0 = absent; 1 = present. Helical thickenings have been recorded in the vessel elements of all species of the *Carmichaelia* complex (Chapter 4), and are reported here for *Swainsona novae-zelandiae* (Fig. 6.1, 6.2). They are absent from the outgroup species and Australian species of *Swainsona* (Fig. 6.3, 6.4), and *Clianthus puniceus* has vessel elements with and without helical thickenings (Fig. 6.5).

11. Vessel element length. 0, 1 ... 9. This continuous character is scored by polymorphism overlap coding for the *Carmichaelia* complex only (see Appendix 6). Most data was taken from the wood anatomy study (Chapter 4), but some species had to be specially examined using the same protocol as that described in Chapter 4. For each species 25 measurements were made. The length of the vessel elements varied between 35 and 271 μm.

12. Ray parenchyma cells. 0 = heterocellular; 1 = homocellular. *Carmichaelia* and *Corallospartium* have rays with heterocellular cells whereas those of *Chordospartium* and *Notospartium* are homocellular (see Chapter 4). *Swainsona decurrens*, *S. formosa*, and *Sutherlandia frutescens* also have heterocellular ray cells.

13. Ray diameter. 0 = up to 4 cells wide; 1 = up to 20 cells wide. Wide rays are characteristic of the New Zealand species (see Chapter 4). This character could be

associated with the presence of pith which is shared by a similar set of species (all the New Zealand taxa). However, it is included as an independent character as many plants with pith also have narrow rays. Australian *Swainsona*, *Lessertia perennans*, and *Sutherlandia frutescens* have rays 1-3(-4) cells wide (Fig. 6.6).

14. Secondary phloem fibres. 0 = straight; 1 = flexuose. These are flexuose and narrow (Fig. 6.7) in all the New Zealand species, and broad and straight (Fig. 6.8) in all other species.

15. Phloem stone cells. 0 = absent; 1 = scarce; 2 = abundant. This feature was first recorded by Slade (1952) for *Notospartium* and *Chordospartium*. Stone cells are also scarce in *Ca. odorata* and *C. crassicaule*.

16. Secondary xylem fibres. 0 = 601-1500 μm long; 1 = < 600 μm long; 2 = > 1501 μm long. This character basically segregated into two categories (0, 1), but a third was necessary to accommodate *S. novae-zelandiae* and *S. oroboides* which had exceptionally long fibres. Most data were taken from the wood anatomy study (Chapter 4), but some species had to be specially examined using the same protocol as that described in Chapter 4. For each species 25 measurements were made.

17. Maximum inflorescence length. 0 = < 99 mm; 1 = 100-199 mm; 2 = 200-299 mm; 3 = > 300 mm. This character is very difficult to code, but there are obvious differences among the terminal taxa. The outgroups and *Swainsona* generally have long inflorescences, whereas as those of the *Carmichaelia* complex are much shorter. Maximum lengths were taken from the *Carmichaelia* descriptions provided in Chapter 3, Thompson (1993), and herbarium specimens.

18. Maximum flower number per inflorescence. 0 = > 20; 1 = 13-19; 2 = 8-11; 3 = 1-7. This character varies among the terminal species, with species of *Swainsona*, *Chordospartium*, *Notospartium*, and several species of *Carmichaelia* having > 20 flowers per inflorescence. The remaining species segregate into several smaller groups.

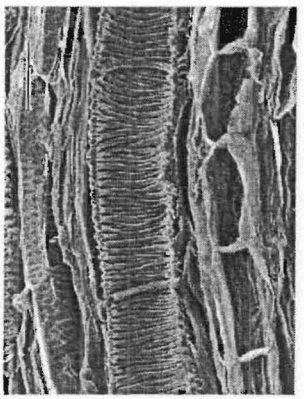

Fig. 6.1

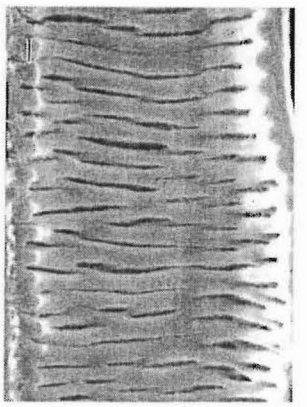

Fig. 6.2

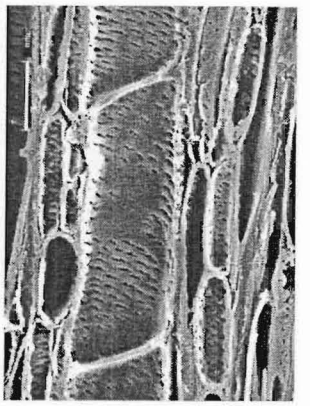

Fig. 6.3

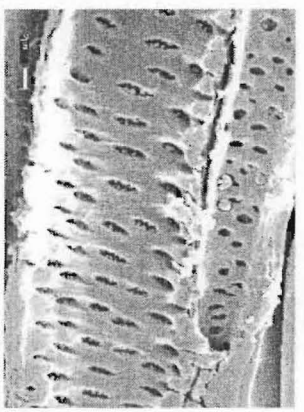

Fig. 6.4

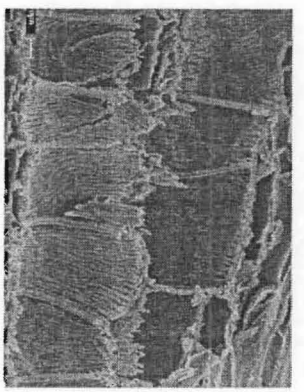

Fig. 6.5

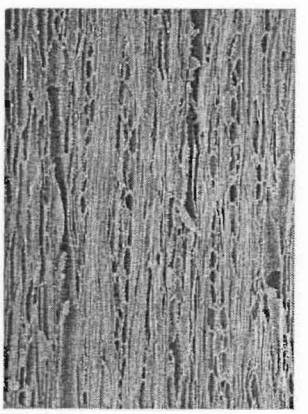

Fig. 6.6

Fig. 6.7

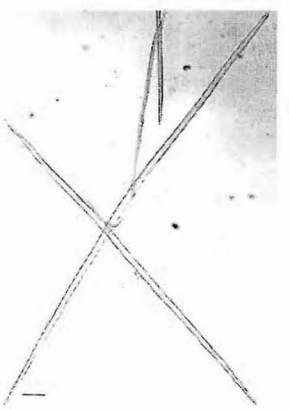

Fig. 6.8

Fig. 6.1-6.8 Anatomical features. Scale bars: Fig. 6.1-6.6 (SEM) = 20 μm; Fig. 6.7, 6.8 (macerations) = 125 μm. **Fig. 6.1, 6.2** *Swainsona novae-zelandiae* vessel elements with helical thickenings. **Fig. 6.3, 6.4** *Swainsona galegifolia* vessel elements without helical thickenings. **Fig. 6.5** *Clianthus puniceus* vessel elements with (left column) and without (right column) helical thickenings. Lower left vessel (arrow) with and without helical thickenings. **Fig. 6.6** *Swainsona galegifolia* rays 1-4 cells wide, transverse longitudinal section. **Fig. 6.7** Flexuose and narrow phloem fibres of *Corallospartium crassicaule*. **Fig. 6.8** Broad and rigid and phloem fibres of *Swainsona galegifolia*.

19. Inflorescence type. 0 = simple; 1 = branched. *Chordospartium*, *Corallospartium*, and *Notospartium torulosum* often have branched racemes.

20. Number of inflorescences per leaf axil. 0 = one; 1 = one or more. The majority of species in the *Carmichaelia* complex have one or more inflorescences per axil.

21. Inflorescence orientation. 0 = erect; 1 = spreading; 2 = drooping. This character was difficult to categorise but the inflorescences of *Swainsona* and many species of the *Carmichaelia* complex are generally erect, whereas some species of the *Carmichaelia* complex have both erect and spreading inflorescences. The inflorescence of *Clianthus* droops.

22. Calyx hairs. 0 = absent; 1 = appressed; 2 = spreading. Hairs appressed to the calyx are characteristic of most species, but in *Chordospartium*, *Corallospartium*, and three species of *Swainsona* they are loose and spreading away from the calyx.

23. Standard modifications of calli or boss. 0 = absent; 1 = present. Modifications to the standard are characteristic of all species of *Swainsona* included in this study (Thompson 1993).

24. Wing length compared to keel length. 0 = wing shorter than keel; 1 = wing longer than keel.

25. Keel shape. 0 = Heenan (1995, fig. 1a); 1 = Heenan (1995, fig. 1b); 2 = Heenan (1995, fig. 1c; 1996, fig. 2a); 3 = Heenan (1996, fig 2b); 4 = Heenan (1996, fig. 2c); 5 = Heenan (1996, fig. 2d); 6 = Heenan (1996, fig. 2e); 7 = Heenan (1996, fig. 2f). Keel shape is characterised for the *Carmichaelia* complex as it provides support for several species groups. This feature was not recorded for *Swainsona* and the outgroup species due to the limited availability of flowering specimens.

26. Keel length. 0, 1 ... 9. This continuous character is scored by polymorphism overlap coding only for the *Carmichaelia* complex (see Appendix 7). Not recorded for *Swainsona* and the outgroup species due to the limited availability of flowering

specimens. Keel length varied between 3.3-29.0 mm.

27. Anther. 0 = bilocular; 1 = unilocular. Unilocular anthers occur in *Carmichaelia* (Godley 1980).

28. Style beard. 0 = absent; 1 = present. All species of *Swainsona* studied are bearded (Thompson 1993), as are several species of the *Carmichaelia* complex (see Chapter 3), and the outgroup *Lessertia perennans* and *Sutherlandia frutescens*.

29. Style modification. 0 = absent; 1 = present. Many species of Australian *Swainsona* (Thompson 1993) and *Notospartium* have modifications to the style such as twisting and geniculate apices.

30. Ovary surface. 0 = glabrous; 1 = hairy. Hairy ovaries occur in *Chordospartium* and *Corallospartium*, and they are also a feature of most species of *Swainsona*.

31. Ovule number. 0, 1 ... 9. This continuous character is scored by polymorphism overlap coding. Scored only for the ingroup because of the limited availability of plant material for the other species (see Appendix 8). The mean and standard deviation were calculated for 10 flowers from three different plants. Ovule number varied between 3-18.

32. Ovule position. 0 = overlapping; 1 = not overlapping. Ovules are in two rows and overlap in all species except *N. carmichaeliae* and *N. torulosum* where they do not overlap and are in a single row.

33. Fruit length. 0, 1 ... 9. This continuous character is scored by polymorphism overlap coding. Scored only for the ingroup because of the limited availability of plant material for the other species (see Appendix 9). The mean and standard deviation were calculated for 10 fruits from three different plants. The fruit length varied between 3-34 mm.

34. Fruit cross–section. 0 = lateral compression; 1 = dorsiventral compression.

Dorsiventrally compressed or inflated fruit occur in all species of *Swainsona* (Thompson 1993) and *Ca. compacta*, *Ca. curta*, and *Ca. juncea*.

35. Fruit replum. 0 = absent; 1 = present. A replum is a synapomorphy for the *Carmichaelia* complex. This is obvious in *Carmichaelia*, and present but less obvious in *Chordospartium*, *Corallospartium*, and *Notospartium*.

36. Fruit valve thickness. 0 = thin; 1 = woody.

37. Fruit fibre orientation. 0 = two directions; 1 = one direction. Fibres oriented in a single direction occur in *Clianthus* and the *Carmichaelia* complex, whereas several species of *Swainsona* and the outgroup species have fibres oriented in two directions (Heenan 1997).

38. Fruit orientation. 0 = spreading; 1 = erect; 2 = drooping.

39. Fruit suture. 0 = not intruded; 1 = intruded. The suture is intruded in some species of *Swainsona*.

40. Fruit beak. 0 = apical; 1 = upturned, or on ventral suture.

41. Fruit constrictions (torulose). 0 = absent; 1 = present. *Biserrula pelecinus* and *N. carmichaeliae* and *N. torulosum* have the fruit wall constricted between the seeds.

42. Fruit valve dehiscence. 0 = indehiscent; 1 = apical dehiscence; 2 = complete dehiscence; 3 = basal dehiscence; 4 = partial lateral attachment. Fruit dehiscence types are characteristic of species groups within the *Carmichaelia* complex; only the *Carmichaelia* complex is examined because of the limited availibilty and quality of fruits for the other species.

43. Seed testa. 0 = well developed; 1 = poorly developed. The testa of *Ca. arborea* and *Ca. odorata* is very thin and poorly developed.

44. Seed length. 0, 1 ... 9. This continuous character is scored by polymorphism overlap coding. Scored only for the ingroup species because of the limited availability of plant material for the other species (see Appendix 10). The mean and standard deviation were calculated for 10 seeds from three different plants. Seed length varied between 1.2-5.1 mm.

45. Seed dehiscence. 0 = shed; 1 = retained. Coded only for the ingroup species because of the lack of suitable material for the other species. Seeds are retained when they remain attached to the fruit by the funicle when the fruit is mature.

46. Radicle. 0 = no fold; 1 = folded. In the seed the radicle of *Chordospartium*, *Corallospartium*, *Notospartium*, and several species of *Carmichaelia* has a pronounced folding.

47. Chromosome number, $2n$. 0 = 16, 24; 1 = 32; 2 = 96. The diploid number of $2n$ = 32 is characteristic of the Australian and New Zealand *Chordospartium*, *Clianthus*, *Corallospartium*, *Notospartium*, most species of *Carmichaelia* (Slade 1953; Hair & Beuzenberg 1959; Purdie 1985; Dawson 1989, 1995) and those species of *Swainsona* (Cooper 1936; Hair 1963; Sands 1975) that have been counted. *Ca. corrugata* and *Ca. uniflora* are hexaploid ($2n$ = 96) (Dawson 1989), and the outgroups are $2n$ = 16 (Polhill 1981; Kreuter 1929, 1930) and $2n$ = 24 (Barneby 1964).

6.2.3 Analysis

The data matrix (Appendix 5) was analysed by parsimony using PAUP Version 3.1.1 (Swofford 1993). Options used include MULPARS, TBR swapping, RANDOM addition sequence, ACCTRAN, `steepest decent off', and `collapse on'. MULPARS saves all of the equally most parsimonious trees; TBR swapping refers to tree bisection-reconnection and is a branch swapping algorithm that bisects a tree along a branch and then the subtrees are reconnected by joining a pair of branches, one from each subtree; RANDOM addition sequence has a randon starting point for the initial search trees; ACCTRAN favours character state reversals rather than parallelisms; steepest descent off only swaps on trees of the same length until a shorter tree is found; collapse on

makes a polytomous node dichotomous to prepare the tree for branch-swapping.

All characters are unordered and polymorphic characters are interpreted as uncertain. Character evolution was analysed with MacClade (Maddison & Maddison 1992). Australian *Swainsona* and *S. novae-zelandiae* were also topologically constrained ('constraint analysis') to a monophyletic group to establish the number of steps necessary for such monophyly. Four redundant species (*Ca. monroi*, *Ca. vexillata*, *Ca. uniflora*, and *Sutherlandia frutescens*) were filtered by MacClade. These were considered redundant even if the character states were not identical as long as a resolution of missing or uncertain data could make them identical (Maddison & Maddison 1992). Each of these species has been added to the phylogenetic trees with their associated species.

The five continuous quantitative characters were removed from the matrix and the data reanalysed to assess the influence of those characters on species relationships, particularly within the *Carmichaelia* complex. In addition, *a posteriori* character weighting using the rescaled consistency index and the maximum value (best fit) was used to develop better resolved evolutionary hypotheses. These analyses were applied to the complete character set and to the character set with quantitative characters excluded. Reweighting continued until the reweighting values, tree topology, and tree length exactly repeated on 2 separate analyses. Appendix 11 summarises information for the reweighted trees, including the number of states per character, the number of steps for each character, rescaled consistency indices, and the weighting values.

Ensemble consistency indices (CI) (Kluge & Farris 1969), retention indices (RI), and rescaled consistency indices (RC) (Farris 1989) are presented. Bootstrap analysis (Felsenstein 1985; Sanderson 1989b) of 1000 replicates with a maximum trees setting of 100 provide a measure of support for particular branches.

6.3 RESULTS AND DISCUSSION

6.3.1 Trees generated

The random addition sequence analysis generated two islands (Maddison 1991) of trees of 175 steps. One island produced 403 and 407 trees, and the other island 908, 909, 910, 911, 912, 913, 916, and 917 trees. The variable number of trees in each island is an uncommon occurrence which results from the manner in which PAUP branch

rearranging algorithms search if zero-length branches are collapsed (Maddison 1991). A strict consensus of the set of trees generated by combining island-917 and island 407 is shown in Fig. 6.9 (CI = 0.46, RI = 0.79, and RC = 0.36). This combined data matrix was reweighted three times by the RC before the tree topology, tree length, and reweighting values exactly repeated producing a set of 9 trees, a strict consensus of which is shown in Fig. 6.10.

For the *Carmichaelia* complex only, a strict consensus tree of island-917 (Fig. 6.11A) and island-407 (Fig. 6.11B) is also presented. When the five continuous quantitative characters were removed from the data matrix 6025 trees with a length of 143 steps were generated (Fig. 6.11C; CI = 0.51, RI = 0.83, and RC = 0.42). The data were reweighted four times to produce an identical tree topology and reweighted values on 77 trees, and a strict consensus of these is shown in Fig. 6.11D.

Tree topology and species relationships for *Swainsona* and *Clianthus* are identical in the consensus trees of the unweighted data (Fig. 6.9, 6.11A, 6.11B, and 6.11C), but these relationships are illustrated only in Fig. 6.9. The two weighted analyses have the same topology and species relationships for *Swainsona* and *Clianthus* (Fig. 6.10 is therefore representative of Fig. 6.11D), but each has different relationships within the *Carmichaelia* complex.

6.3.2 Major clades

The consensus trees of all analyses show two major clades, a clade including only Australian species of *Swainsona* and the other a New Zealand clade (e.g., Fig. 6.9). The New Zealand clade includes the three minor clades *S. novae-zelandiae*, *Clianthus puniceus*, and the *Carmichaelia* complex.

The characters that support the New Zealand clade are closely associated with the stem anatomy of the group. For example, the New Zealand taxa are woody shrubs or subshrubs with terminal innovation shoots, persistent stem pith, vessel elements with helical thickenings, ray parenchyma up to 20 cells wide, and slender and flexuose phloem fibres. In addition, their inflorescences are less than 100 mm long. In comparison, Australian *Swainsona* and the outgroup species are annual, herbaceous, or short-lived shrubs with mainly basal innovation shoots, they lack stem pith, their vessel elements are without helical thickenings, their ray parenchyma is 1-4 cells wide, and

they have broad and rigid phloem fibres.

6.3.3 *Carmichaelia* complex phylogeny

The *Carmichaelia* complex is supported by four synapomorphies: fruit with a replum; habit-heteroblastic development (exceptions are *Ca. astonii*, *Ca. exsul*, *Ca. nana*, and *Ca. williamsii* which are considered to have lost this feature); flat pith (apart from *Ca. kirkii* which has round pith); leafless adult plants (partial exceptions are *Ca. arborea* and *Ca. odorata* which are sometimes leafy).

Within the *Carmichaelia* complex several species groups are recognised (e.g., Fig. 6.9, 6.10), and some of these correspond to either currently accepted genera or the subgeneric groups of Simpson (1945). For example, *Notospartium* (bootstrap value = 85%); *Ca. compacta/Ca. curta/Ca. juncea* (subg. *Huttonella*, bootstrap value = 76%); *Ca. arborea/Ca. odorata* (subg. *Thompsoniella*, bootstrap value = 90%); *Ca. astonii/monroi/vexillata* (subg. *Monroella*, bootstrap value = 83%); and *Ca. corrugata/Ca. uniflora* (subg. *Suterella*, bootstrap value = 98%). *Chordospartium* and *Corallospartium* form a trichotomy (bootstrap = 76%) which is unresolved because several characters of *Corallospartium* and *Ch. muritai* are shared with *Carmichaelia* (Table 6.1). The *Chordospartium* and *Notospartium* branches are sister groups and have 78% bootstrap support.

The two islands of trees have significantly different topologies and species relationships within the *Carmichaelia* complex. Island-917 (Fig. 6.11A) has relatively well-resolved terminal relationships, but basal polytomies are an indication of poorly resolved relationships and the lack of accumulated synapomorphies (for other basal polytomies see also Fig. 6.11C). Although island-917 is poorly resolved at the base of the *Carmichaelia* complex, the largest clade (Fig. 6.11A, clade B)arising from this polytomy has a relatively well defined bifurcating topology. This clade is supported by a glabrous style and, with the exception of *Ca. williamsii*, by the wing being longer than the keel. Island-407 has a clade comprising the same set of species but, in comparison to island-917, the relationships of these are poorly resolved (Fig. 6.11A, clade D). However, at the base of the *Carmichaelia* complex island-407 (Fig. 6.11B) is better resolved than island-917 (Fig. 6.11A). The strict consensus tree (Fig. 6.9) produced by combining both islands provides a conservative phylogenetic hypothesis, and although

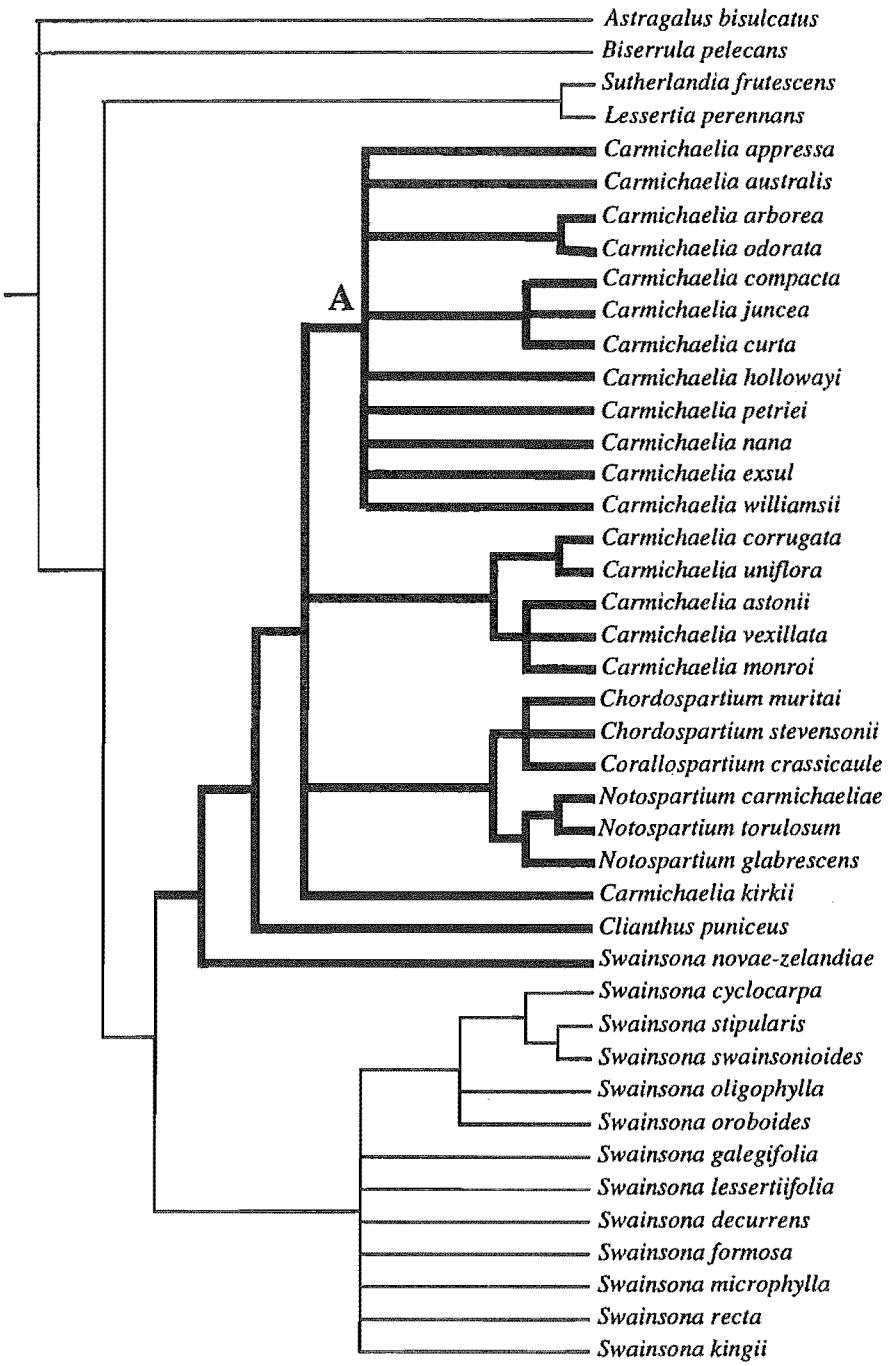

Fig. 6.9 Strict consensus tree of 1324 trees (island-917 and island-407 combined). Clade A is characterised by a glabrous style.

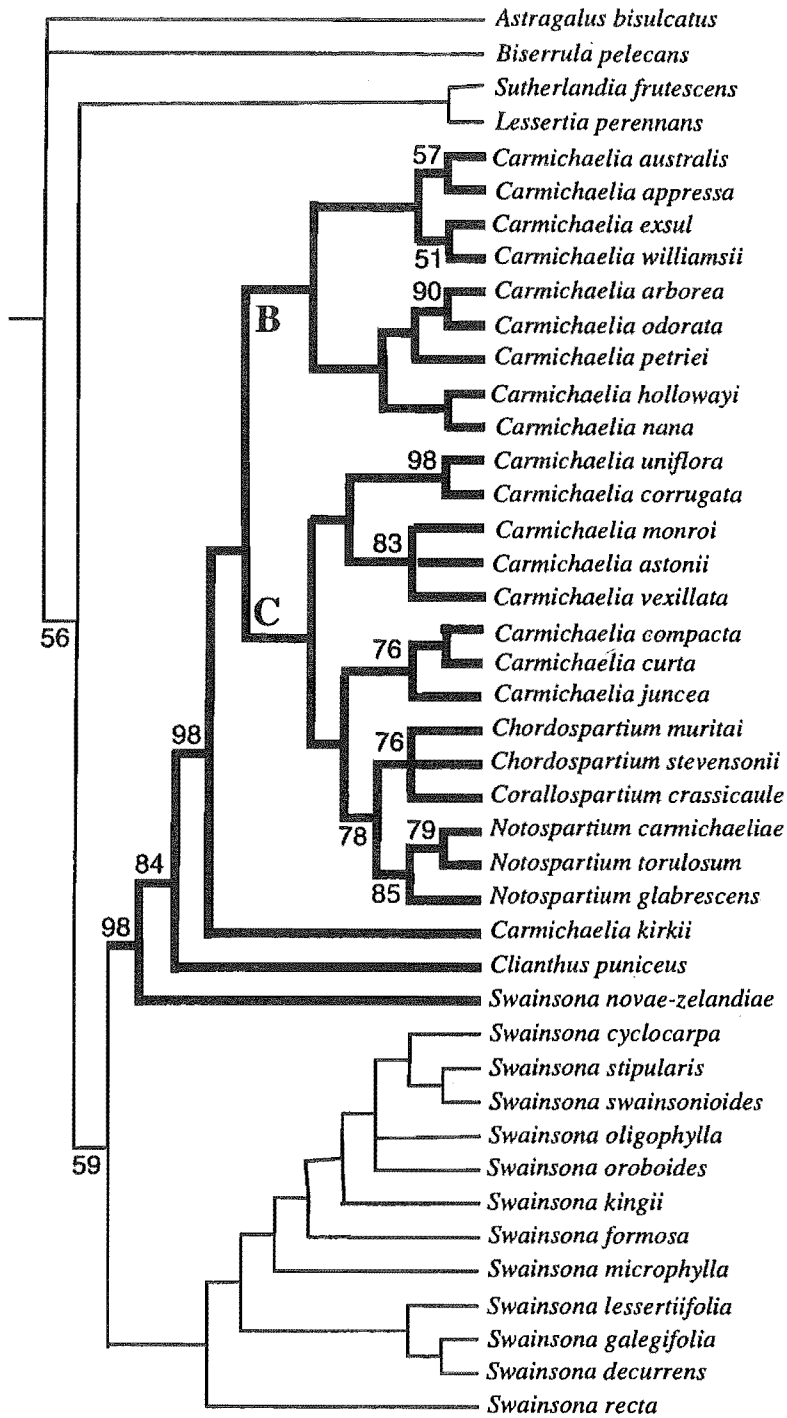

Fig. 6.10 Strict consensus tree of the 9 shortest trees derived by reweighting the 175 step trees by the rescaled consistency index (CI = 0.46; RI = 0.81; RC = 0.37). Clade B is supported by a dehiscent fruit. Clade C is characterised by indehiscent fruit. Bootstrap values above 50% provide support for several clades.

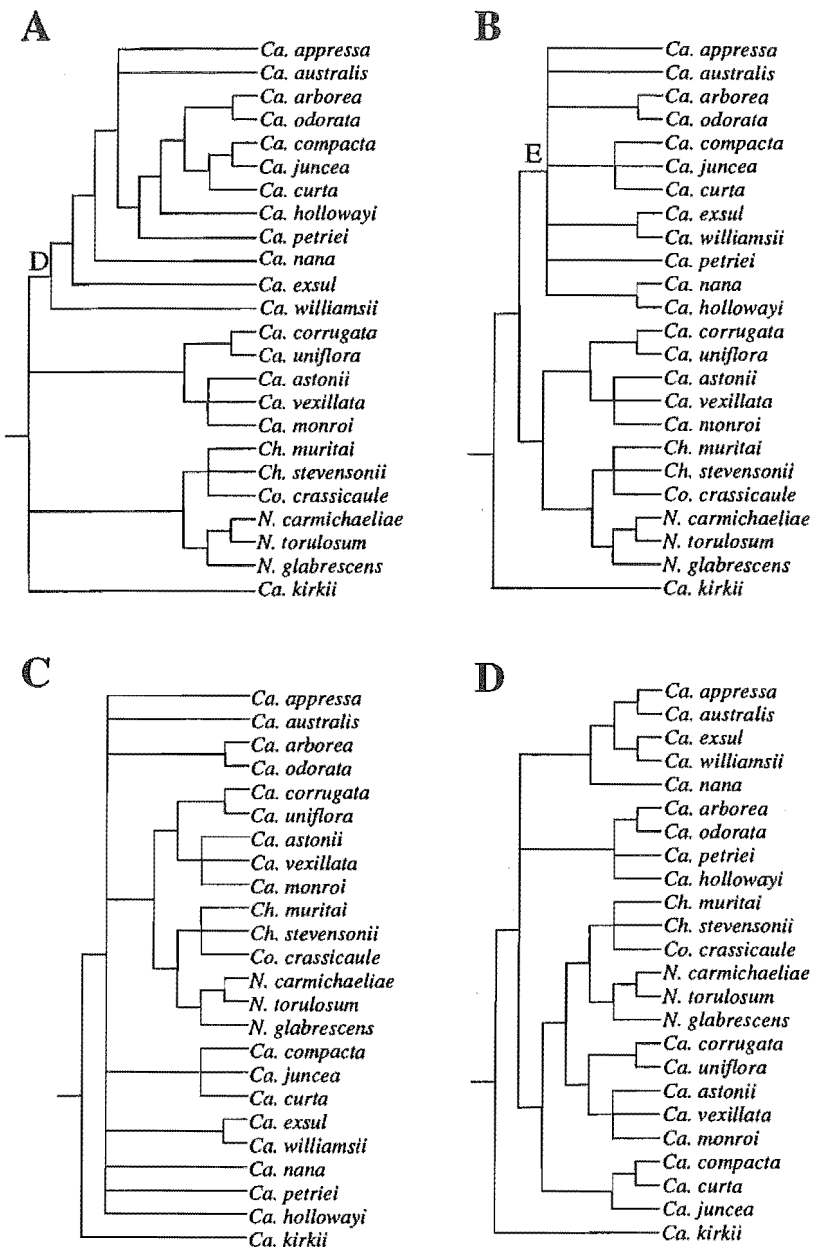

Fig. 6.11 Strict consensus trees of the *Carmichaelia* complex derived from different analyses: **A**, island-917 derived from random addition sequence (clade D comprises the same species as Fig. 6.9 clade A); **B**, island-407 derived from random addition sequence (clade E comprises the same species as Fig. 6.9 clade A); **C**, 6025 trees derived from closest addition sequence minus 5 quantitative characters; **D**, 77 trees derived from closest addition sequence, minus 5 quantitative characters, and reweighted.

recognising four main clades it provides little resolution at the base of the *Carmichaelia* complex.

A rapid series of dichotomous branching events or a single polytomous event is likely to result in the lack of a well defined (i.e., bifurcating) phylogenetic hypothesis (Hoelzer & Melnick 1994). The reason given for this by Hoelzer & Melnick (1994) is that "ancestral forms represented by sequential nodes on a phylogenetic tree would have little time to diverge between speciation events." Therefore, the presence of polytomous nodes in this analysis can be considered as phylogenetic hypotheses in the same way as bifurcating topologies (Hoelzer & Melnick 1994). Maddison (1989) has also referred to this type of interpretation as multiple speciation events or `hard polytomies'. It is plausible that a rapid or recent radiation occurred in the *Carmichaelia* complex and that this resulted in the formation of species and species-groups that share few characters in common with other groups at either basal or terminal positions (e.g., Fig. 6.9).

An improved resolution of species relationships within the *Carmichaelia* complex is illustrated by the weighted analysis of the combined 1324 trees from island-917 and island-407 (Fig. 6.10). In the strict consensus of these trees *Ca. kirkii* is sister species to the rest of the *Carmichaelia* complex, as it also is in the strict consensus trees of island-407 (Fig. 6.11B) and when the five quantitative characters are excluded (Fig. 6.11C, 6.11D). *Carmichaelia kirkii* is supported in this position by having round pith, a feature it shares with *Clianthus* and *Swainsona*. Interestingly, *Ca. kirkii* is part of a polytomy in the strict consensus of island-917 (Fig. 6.11A) and in the consensus tree of the combined islands (Fig. 6.9).

Carmichaelia is further split into two large clades (Fig. 6.10, clades B and C), with clade C being characterised by indehiscent fruit - excluding *Ca. corrugata/Ca. uniflora* in which the fruits are weakly dehiscent at the base. It is significant that *Ca. compacta /Ca. curta/Ca. juncea* are associated with the *Chordospartium*, *Notospartium*, and *Ca. astonii* clades (see also Fig. 6.11D). In contrast, in the unweighted trees (Fig. 6.9, 6.11A, 6.11B) these species are associated with species that have glabrous styles and the keel longer than the wings. Therefore, the placement of *Ca. compacta /Ca. curta/Ca. juncea* in the weighted trees is in contradiction to the conservative, unweighted, strict consensus trees. Weighting in these analyses (Fig. 6.10, 6.11D) appears to have given particular emphasis to fruit characters. Clade B (Fig. 6.10) includes those species with a glabrous style, the wings being longer than the keel

(excluding *Ca. williamsii*) and dehiscent fruit.

A notable feature of island-407 (Fig. 6.11B), and the reduced character phylogenetic hypotheses (Fig. 6.11C, 6.11D), is the sister group relationship of the low shrubby *Ca. astonii/Ca. corrugata* group and the large shrubby and tree-like *Chordospartium/Notospartium* clades. These species share hairy styles and the keel being longer than the wings, and yet they have contrasting growth forms that may represent radiations into different adaptive zones. The tree-like *Chordospartium* and *Notospartium* mainly occur among tall shrubs and on forest margins in riparian habitats in Marlborough, whereas the dwarf species of *Carmichaelia* occur with herbs and other dwarf shrubs in the dry eastern mountains on or around the margins of rocky outcrops, and on river terraces, outwash fans, and glacial moraine.

The reduced character set phylogenetic hypotheses (Fig. 6.11C, 6.11D) differ from the other topologies in that the species which are included in clade A of the combined islands (Fig. 6.9), clade D of island-917 (Fig. 6.11A), and clade E of island-407 (Fig. 6.11B) have collapsed to form polytomies with clades comprising *Chordospartium/Notospartium* and *Ca. astonii/Ca. corrugata*. Thus, inclusion of quantitative characters provided a better resolution of relationships among the species with a glabrous style and wings longer than the keel.

The subshrub *Ca. nana* does not have a close relationship to the other low growing species of the *Ca. astonii/Ca. corrugata* group, implying that its growth form and unifoliolate leaves have evolved independently (e.g., Fig. 6.9, 6.10). The small keel, wings longer than the keel, and glabrous style are features that *Ca. nana* shares with *Ca. arborea*, *Ca. odorata*, *Ca. petriei*, *Ca. appressa*, *Ca. australis*, and *Ca. exsul*, and its placement with those species is therefore appropriate. In contrast, the *Ca. astonii/Ca. corrugata* group has a large keel and the wings are shorter than the keel.

The unresolved relationships indicated by the trichotomy of *Co. crassicaule*, *Ch. stevensonii*, and *Ch. muritai* (Fig. 6.9, 6.10) are noteworthy as *Ch. muritai* and *Co. crassicaule* each share several different features with both *Ch. stevensonii* and species of *Carmichaelia*. *Corallospartium crassicaule* is similar to *Ca. kirkii* in having a relatively large flower, bearded style, and a strongly reflexed standard, and with other species of *Carmichaelia* it shares bi- or trifoliolate leaves and heterogeneous ray cells. Characters shared with *Ch. stevensonii* include grooved stems (Slade 1952), heteroblastic and mainly unifoliolate leaves, and the obliquely obovate, hairy, and

indehiscent pod. *Chordospartium muritai* also combines characters of several genera in having a glabrous style like several species of *Carmichaelia* and, as noted by Purdie (1985), it has the growth habit of *Notospartium*, flower colour and size of *Carmichaelia* (particularly species of the lower part of clade D, Fig. 6.11A), and the pods and grooved branches of *Ch. stevensonii* and *Corallospartium.* These characters of *Co. crassicaule* and *Ch. muritai* suggest intermediacy between *Carmichaelia* and *Ch. stevensonii* and this could be interpreted as either evolutionary intermediate forms or that these species originated by hybridisation.

The relationships of *Ca. hollowayi*, *Ca. nana*, and *Ca. petriei* are also of special interest. *Carmichaelia hollowayi* is either sister species to *Ca. nana* (Fig. 6.10, 6.11B), indirectly related to *Ca. nana* or *Ca. petriei* (Fig. 6.11A), sister species to *Ca. petriei* (Fig. 6.11D), or part of a polytomy (Fig. 6.9, 6.11C). It is possible that *Ca. hollowayi* may have evolved from hybridisation and that its variable position in the trees is a result of the putative parents being *Ca. nana* and *Ca. petriei.* Its growth habit is intermediate between the dwarf *Ca. nana* and the shrubby *Ca. petriei*, the fruit valves are flattened as in *Ca. nana* but they are weakly dehiscent in a similar manner to *Ca. petriei*, and the flowers are of similar dimensions to *Ca. petriei.* A putative *Ca. nana* × *Ca. petriei* hybrid from the Waitaki River valley has pods which are very similar to *Ca. hollowayi* (CHR 510595).

McDade (1990) reported on the influence of hybrids in phylogenetic analyses and concluded that hybrids may be placed nearest to their most derived parent or as basal clades in the lineage that includes their most derived parent. The position of the species of putative hybrid origin, *Ch. muritai* and *Co. crassicaule*, suggests that they have aligned themselves with *Ch. stevensonii*, the putative parental species with which they share several derived features. In contrast, the position of *Ca. hollowayi* is unstable but, significantly, it is never basal to both of the two putative parents.

The first phylogeny of the *Carmichaelia* complex was proposed by Slade (1952, 1953) on the basis of pith type and leaf trace systems. Slade (1952) postulated that *Ca. kirkii* with round pith and trilacunate nodes was the "ancestral type" of the *Carmichaelia* complex. *Carmichaelia kirkii* is sister group to all other species of *Carmichaelia* in several of the phylogenetic hypotheses presented here (Fig. 6.10, 6.11B, 6.11C, 6.11D). The overall flowchart phylogeny proposed by Slade (1953, fig. 2) bears only slight similarity to two of the phylogenetic hypotheses presented here, those of Fig. 6.10 and

6.11D. These phylogenetic hypotheses are similar in that the *Ca. compacta* branch is sister group to the *Chordospartium/Notospartium* alliance. A major difference is that Slade considers Simpson's (1945) subgenus *Carmichaelia* (e.g., *Ca. australis*) to be basal to *Ca. williamsii* and *Ca. nana*, whereas in several of the phylogenetic hypotheses presented here these species are basal to or are sister species to *Ca. australis* (e.g., Fig. 6.9, 6.10, 6.11A, 6.11D).

The *Carmichaelia* complex and *Clianthus* have fruit fibres oriented in one direction (Heenan 1997), a feature suggesting a close relationship. However, *Clianthus* is distinguished from the *Carmichaelia* complex by vessel elements with and without helical thickenings, drooping inflorescences, and a follicle fruit (Godley 1979).

6.3.4 Biogeography

The phylogenetic hypotheses presented here indicate strong support (98% bootstrap) for a monophyletic New Zealand clade of *Swainsona novae-zelandiae*, *Clianthus puniceus*, and the *Carmichaelia* complex. The *Carmichaelia* complex also has 98% bootstrap support as a monophyletic group and, with the exception of *Ca. exsul* from Lord Howe Island, is restricted to New Zealand. *Carmichaelia exsul* is likely to have dispersed to Lord Howe Island relatively recently as it is among the derived members of *Carmichaelia*. The South Island has been an important place of evolution for the *Carmichaelia* complex as 22 of the 23 species endemic to New Zealand occur in the South Island, and only 5 occur in the North Island. Of the North Island species, *Ca. nana*, *Ca. odorata*, *Ca. juncea*, and *Ca. australis* are shared with the South Island, and *Ca. williamsii* is restricted to the northern half of the North Island. It is notable that all of the North Island species, and *Ca. exsul*, occur on the same clade (e.g., Fig. 6.9, clade A; Fig. 6.10, clade B). Within the South Island, Marlborough is a centre of diversity with 5 endemic species (*Ca. astonii*, *Ch. muritai*, *Ch. stevensonii*, *N. carmichaeliae*, and *N. glabrescens*), Otago has 3 endemics (*Ca. compacta*, *Ca. curta*, and *Ca. hollowayi*), and Canterbury has 2 (*Ca. appressa* and *N. torulosum*).

The phylogenetic position of the scree specialist *Swainsona novae-zelandiae* is particularly enigmatic in that it is sister species to the rest of the New Zealand clade. As a sister group it is very surprising that it has not radiated into other scree-like habitats such as glacial moraines, outwash fans, and alluvial river terraces. This is in contrast to

the 23 species of the *Carmichaelia* complex that are likely to have radiated during the Late Miocene and Pliocene in response to cold and dry conditions and when new habitats arose during the Kaikoura Orogeny (Andrews 1914; Raven 1973; Chapter 4). If this scenario is accepted then a very rapid radiation occurred in the *Carmichaelia* complex with an apparent stasis or extinction in the sister species *S. novae-zelandiae*. *Clianthus puniceus* also arises near the base of the New Zealand clade and its leafy habit, moderate hardiness, lowland forest habitat, and now restricted distribution are consistent with having evolved earlier in the Tertiary when conditions were warmer and more favourable. Therefore, its present restricted distribution may be a result of the colder temperatures which have occurred since the Late Miocene. A single fossil of *Ca. australis* is known from the Late Pliocene Waipaoa Series (Oliver 1928), and this is consistent with a relatively recent origin for the group.

The position of *S. novae-zelandiae* on the New Zealand clade implies that the more derived *Clianthus* has lost the character of all vessel elements having helical thickenings, as it has vessel elements both with and without helical thickenings. As an alternative, if *Clianthus* was sister species to the rest of the New Zealand clade its vessel elements with and without helical thickenings could be considered a progression from *Swainsona* and the outgroups species in which they are absent, through to the *Carmichaelia* complex and *S. novae-zelandiae* where they are well developed. This would mean that *S. novae-zelandiae* and *Carmichaelia* complex would share a common ancestor whose vessel elements had well developed helical thickenings. With *S. novae-zelandiae* in a basal position on the New Zealand clade *Clianthus* would have to lose vessel element helical thickenings, whereas if *Clianthus* was basal *S. novae-zelandiae* would need to develop fruit fibres oriented in two directions after *Clianthus* had lost this feature. Examination of the only other member of the Carmichaelieae, the extinct and monotypic *Streblorrhiza speciosa* from Phillip Island in the Tasman Sea, may help resolve some of the problems outlined above.

Sanderson & Liston (1995), using molecular data, suggested that the evolution of the Southern Hemisphere galegoid legumes occurred along geographic lines for Australia, New Zealand, and South Africa. This pattern is supported by the present analysis of morphological and anatomical characters (Fig. 6.9, 6.10). The woody New Zealand clade of *Swainsona novae-zelandiae*, *Clianthus puniceus*, and the *Carmichaelia* complex would almost have certainly evolved from a herbaceous ancestor as the sister

group and outgroups in this analysis, and the sister groups in the molecular work of Liston & Wheeler (1994), Sanderson & Liston (1995), and Sanderson & Wojciechowski (1996) are herbaceous. The place of origin of this ancestor is difficult to determine from the present analysis, but the sister group relationship of Australian *Swainsona* and the New Zealand clade (Fig. 6.9; e.g., Sanderson & Liston 1995) implies that these legumes shared a common ancestor. Andrews (1914) suggested a tropical origin for *Carmichaelia*, and that it came to New Zealand either by a tropical land route or as a sea waif. A Malayan origin for *Carmichaelia* was advocated by Oliver (1935), who also considered that the group had come to New Zealand by an ancient land connection. More recently (Raven & Polhill 1981; Polhill 1981) it was proposed that the *Carmichaelia* complex was probably derived from ancestors similar to the mainly tropical Tephrosieae, but there is no obvious link to any particular group. Barneby (1964) has suggested that *Swainsona* is very similar to the African *Lessertia* and *Sutherlandia*, and the Asian *Astragalus* subg. *Pogonophace*, and that this group could perhaps be united into a single genus. Although Barneby's view is rather extreme it does highlight the close affinity that exists among the taxa. Therefore, although *Astragalus* subg. *Pogonophace* was not included in the present analysis, it may be from such a group that the progenitor of the Australian and New Zealand taxa was derived.

6.3.5 *Swainsona* phylogeny

Swainsona novae-zelandiae is basal in the New Zealand clade and it is clearly distinguished from Australian *Swainsona* by all the features that support the New Zealand clade: viz., it is a subshrub with terminal innovation shoots, it has persistent stem pith, vessel elements with helical thickenings, ray parenchyma up to 9 cells wide, and slender and flexuose phloem fibres. In comparison the Australian species of *Swainsona* are annuals or short-lived herbaceous perennials, with basal innovation shoots, hollow stems, vessel elements without helical thickenings, ray parenchyma 1-4 cells wide, and broad and rigid phloem fibres. *Swainsona novae-zelandiae* also differs from Australian *Swainsona* by its strongly rhizomatous growth habit, and from the other New Zealand species by its very long secondary xylem fibres. However, unlike the other New Zealand species, and hence its basal position on the New Zealand clade, it is allied to the Australian *Swainsona* by the fruit fibres which are oriented in two

directions.

Among Australian *Swainsona* the clade (Fig. 6.10) below *S. microphylla* has an intruded suture, that below *S. kingii* has 2-11 leaflets, and the branch with *S. oroboides*, *S. oligophylla*, *S. swainsonioides*, *S. stipularis*, and *S. cyclocarpa* has 8-11 flowers and a modified style. Therefore, the general pattern of evolution in Australian *Swainsona* is a reduction of flower and leaflet number, and the acquisition of unique features such as modified styles and intruded sutures.

The herbaceous Australian *Swainsona* clade differs from the herbaceous outgroup species by two characters: the standard of many species is modified with calli and/or a boss and the chromosome number is $2n = 32$ (the New Zealand species also mostly have $2n = 32$). The outgroup species lack modifications to the standard and have a chromosome number of $2n = 16$ or 24. The modification of the standard observed in the 12 Australian species of *Swainsona* included here may not be present in all 84 species of the genus. Australian *Swainsona* and the outgroup species differ from the New Zealand clade in sharing anatomical characteristics such as vessel elements lacking helical thickenings, narrow rays, absence of pith, and broad and rigid phloem fibres. These anatomical characters have been observed in an additional 35 species of *Swainsona* (P. B. Heenan unpubl. data).

When topological constraints were invoked to make Australian *Swainsona* and *S. novae-zelandiae* into a monophyletic group 108 trees of 178 steps were produced, and *S. novae-zelandiae* was in a basal position in the *Swainsona* clade. These trees are three steps longer than the 175 steps required in the most parsimonious results presented here (e.g., Fig. 6.9). *Swainsona novae-zelandiae* was supported in the basal position of the *Swainsona* clade by sharing several characters with a clade of *Clianthus* and the *Carmichaelia* complex. For example, in examining character evolution with MacClade, the extra three steps were gained by the 2-step equivocal homoplasy (rather than a 1-step synapomorphy) of persistent stem pith, vessel elements with helical thickenings, and slender and flexuose secondary phloem fibres that are shared by the *Clianthus/Carmichaelia* complex clade and *S. novae-zelandiae* on the *Swainsona* clade.

6.3.6 Taxonomic consequences

The retention of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and

Notospartium as distinct genera is tenuous given that some characters previously used to define a particular genus also occur in other genera, as do several of the recently recognised characters (e.g., leaf heteroblasty and wood anatomy; Table 6.1). Therefore, on the basis of the characters used for this study *Carmichaelia* is paraphyletic if *Chordospartium*, *Corallospartium*, and *Notospartium* are retained as distinct genera.

The phylogenetic analysis of the *Carmichaelia* complex as represented by the consensus tree (Fig. 6.9) offers three alternative classifications for recognising different monophyletic genera. These are:

- One genus recognised. *Carmichaelia* recircumscribed to include *Chordospartium*, *Corallospartium*, and *Notospartium*.
- Four genera recognised. *Carmichaelia kirkii* placed in a monotypic genus; *Notospartium* recircumscribed to include *Chordospartium* and *Corallospartium*; the *Carmichaelia corrugata/C. astonii* lineage placed in a new genus; *Carmichaelia* sens. strict. (Fig. 6.9, branch A).
- Five genera recognised. *Notospartium* retained; *Corallospartium* recircumscribed to include *Chordospartium*; *Carmichaelia* split into three genera — *C. kirkii*, *C. corrugata/C. astonii* lineage, and *Carmichaelia* sens. strict. (Fig. 6.9, branch A).

The recognition of genera in this study is founded on the principles of evolutionary classification. Therefore, the recognition of particular groups at the rank of genus is based on the distribution of characters, the adaptive significance of the lineages, ancestor-descendant relationships, and other aspects of the general biology of the taxa.

The recognition of four or five segregate genera would maintain a classification in which many of the significant taxonomic characters are shared in different combinations across those genera (Table 6.1). The proposed segregate genera would not be recognised by shared and derived characters from a number of different character types (e.g., wood anatomy, pod type), but would be recognised by a single character type and/or a combination of characters including some that are considered to be ancestral. For example, *Carmichaelia* sens. strict. (Fig. 6.9, branch A) would be recognised by a glabrous style and *Notospartium* by its narrow and linear pods. Furthermore, fruit with a replum, habit-heteroblastism, flat pith (except *Ca. kirkii*), and leafless adult plants would be plesiomorphic character states for each of the segregate genera. These are

significant characters that support the *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* lineage, and they would have little application to any classification if four or five segregate genera were recognised.

Bootstrap values provide little support for the two proposals that recognise a number of segregate genera. The proposed segregate generic groups of *Notospartium*, *Chordospartium/Corallospartium*, and *Chordospartium/Corallospartium/Notospartium* have greater than 50% bootstrap support, but the bootstrap values are only moderate (78–85%) and not considered high enough to support recognition at the rank of genus. There are no biogeographic or other ecological attributes that support any of the segregate genera.

The option to recircumscribe *Carmichaelia* to include *Chordospartium*, *Corallospartium*, and *Notospartium* is based on a number of shared and derived characters (replum, habit-heteroblastism, flat pith, leafless adults) and a very high bootstrap value (98%). This choice has no complications in regard to plesiomorphic characters and it accommodates a significant amount of natural variation such as the styles being glabrous or hairy and different pod types. Furthermore, the enlarged concept of *Carmichaelia* probably represents an adaptive radiation into dry and cold conditions during the Pliocene/Pleistocene. The synapomorphies that support the expanded concept of *Carmichaelia* represent a new lineage that is derived from a leafy ancestor that is probably similar to *Clianthus*. There is a clear ancestor-descendant relationship that is represented by a significant change in characters, and further emphasised by specific ecological requirements and biogeographic attributes.

The *Carmichaelia* subgeneric classifications proposed by Kirk (1899) and Simpson (1945) are substantially unnatural and not supported by the present phylogenetic analysis. Kirk's *Carmichaelia* section *Nana* for the dwarf species is shown to be polyphyletic as *Ca. nana* is always on a different clade from the *Ca. astonii/Ca. corrugata* group of species. Likewise, Kirk's *Eucarmichaelia* is paraphyletic. Several of Simpson's (1945) subgenera are monophyletic (e.g., *Huttonella*, *Kirkiella*, *Suterella*, *Thomsoniella*) while others are not (e.g., *Carmichaelia*, *Enysiella*, *Monroella*, *Petriea*), but the rank of subgenus is severely weakened by a paraphyletic *Carmichaelia*. Indeed, it is not possible to construct an infrageneric classification for the *Carmichaelia* complex because of the distribution of most significant taxonomic characters across different species or species groups (Table 6.1). Although several groups of species are

morphologically well defined, insufficient support for an infrageneric classification is well highlighted by the lack of a consistent topology within the *Carmichaelia* complex among the six cladograms illustrated (Fig. 6.9-6.11). Another aspect of the lack of synapomorphies for particular clades is the ladder-like tree topology and hence ladder-like distribution of characters that supports individual species rather than species groups. This lack of well defined sister species relationships is seen, for example, in Fig. 6.11A (clade D) with *Ca. exsul*, *Ca. williamsii*, and *Ca. nana*.

Swainsona novae-zelandiae is shown to differ from Australian *Swainsona* in growth habit and a number of significant anatomical characters. To reflect the monophyly of Australian *Swainsona* more accurately the very distinctive *S. novae-zelandiae* should be removed and placed in a new monotypic genus.

6.3.7 Usefulness of the phylogenetic analysis

The phylogenetic analysis has proven to be very useful as a method for reconstructing character evolution and establishing relationships among taxa. It has been particularly useful in providing a framework for the development of an evolutionary classification in *Carmichaelia*. A strength of using PAUP and MacClade is that it facilitates the study of character evolution and change.

A notable feature in this particular study is that the application of the phylogenetic (cladistic) principles of classification would be congruent with the evolutionary classification that is proposed. For example, if branching points were used to construct a phylogenetic classification using the strict consensus tree (Fig. 6.9) it would be appropriate to recognise 4 genera: (1) Australian *Swainsona*, (2) *Swainsona novae-zelandiae*, (3) *Clianthus*, and (4) the *Carmichaelia* complex. This cladistic classification, based on the topology of the consensus tree is consistent with the recommendations made for a revised classification based on evolutionary taxonomy principles of classification.

6.3.8 Quantitative characters

The inclusion of quantitative characters in phylogenetic analyses is controversial with arguments both for (Thiele & Ladiges 1988; Chappill 1989; Stevens 1991; Thiele

1993) and against (Mickevich & Farris 1981; Pimentel & Riggins 1987; Felsenstein 1988; Farris 1990) their use. The discussion that follows reviews these arguments and evaluates the application of these procedures for the phylogenetic analysis of *Carmichaelia*.

The main arguments for not including quantitative characters in cladistic analyses are that this class of data is not appropriate as it does not form discrete states and the methods to code data are arbitrary. Furthermore, quantitative characters are considered to have too much homoplasy, are too difficult to describe as statistics are needed, and the branching diagrams are unsuitable for illustrating such data. Continuous characters are often considered to be transformation homologies that are not subject to easy testing, and therefore they are invalid as characters for cladistic analyses. Strict definitions of cladistics state that characters must be multistate variables that are coded as sequential numbers or in additive binary fashon.

Many of the above arguments for not including quantitative characters in phylogenetic analyses are flawed. The only criterion that quantitative characters have to fulfil is that they have homologous character states. Character states can be described by undertaking statistical analyses and coding of data, and these can be tested by parsimony analysis of the data set. Every decision of character state membership is actually an explicit hypothesis of homology. Assuming that quantitative characters will exhibit more homoplasy than discrete characters is an a priori assumption about their quality and usefulness. All characters can be polarized by outgroup comparison.

The use of coding methods such as gap and segment coding to convert raw quantitative data to a coded format has also been criticised. Such codes are considered to have no phylogenetic meaning and the conversion of raw data in to codes involves data massaging. Segment and gap coding are arbitrary in that the number of codes, their distribution, and membership depend on either the a priori number of segments chosen or the critical gap size. Ratios and means of quantitative data have been regarded as phenetic values that can not be scored in groups or polarised by outgroup comparison. However, statistical tests of significance are a biologically relevant way to determine whether two samples are the same. Therefore, coding methods should preferably be based on the central tendency (usually mean or median) of the taxon. Statistical methods based on probability are good summaries of data and provide an objective, repeatable, non-arbitrary method for deciding if two taxa are significantly different in

some measurement attribute.

The main reason for including quantitative characters in phylogenetic analyses is that they may provide extra information on relationships, and that they are a legitimate source of data that should not a priori be excluded. If quantitative characters can be coded using sound statistical methods that are non-arbitrary, objective, and repeatable, then they should be included in phylogenetic analyses.

A pragmatic solution to the problem of including or excluding quantitative characters can be obtained by clearly defining the type of analysis being undertaken. A phylogenetic analysis using cladistic principles would include only characters which can be scored for discrete states. In contrast, a phylogenetic analysis using the methods of evolutionary taxonomy would allow for the inclusion of quantitative characters, as all information is considered to be important in the development of an evolutionary classification. A similar solution has been proposed for autapomorph characters. They are excluded from cladistic phylogenetic analyses, but are included in evolutionary taxonomy phylogenetic analyses (Mayr 1981).

Inclusion of quantitative characters in the evolutionary phylogenetic analysis of *Carmichaelia* is important as several species or species-groups are characterised by particular lengths or a range of measurements. Therefore, the a priori exclusion of such characters would be inappropriate, particularly if they are shown to support particular groups of species rather than evolving independently in several lineages. The application of a method such as polymorphism overlap coding (Sanderson 1989a) provides objectivity and repeatability to the process of assigning character states to a polymorphic character which varies continuously across different species and which lacks discrete states. This method is considered more rigorous than the practice of selecting arbitrarily discrete categories. For example, ovule number could have been divided into several arbitrary categories such as 1-3, 4-8, 8-15, >16. However, this implies that if a species has 4 ovules it shares a closer relationship to a species with 8 ovules than it does to another with 3 ovules. Coding by polymorphism overlap coding allows each species relationships to be determined without a priori assumptions. The inclusion of quantitative characters for advancing better resolved phylogenetic hypotheses that generate fewer equally parsimonious trees is supported by a comparison of Fig. 6.9 (consensus of 917 trees, 47 characters) with Fig. 6.11C (consensus of 6025 trees, 42 characters).

6.3.9 Character weighting

Character weighting procedures have advocates for (Farris 1969; Goloboff 1993) and against (Swofford & Olsen 1990; Maddison & Maddison 1992) their application. As a posteriori successive character weighting procedures were used in this study, and their use had an influence on tree topology and species relationships, it is appropriate to review their application in phylogenetic studies.

A posteriori successive character weighting allows for weights to be assigned to characters based on their fit to trees that were generated by an initial analysis. The aim is to converge on fewer tree topologies by penalising those characters that fit the trees poorly (homoplastic characters) and rewarding characters that fit the trees well (homologous characters). It is the characters themselves that provide the information on which characters are more reliable than others.

Two criticisms have been levelled at the use of a posteriori weighting. Firstly, that the method is circular as the weight for a particular character is determined by the level of homoplasy that the character exhibits in the generation of the initial set of trees. Therefore, the characters that are the most homologous will contribute the most to the weighted tree(s). The second criticism is that trees derived from character weighting should not be used in the contruction of a classification as they may not be particularly stable.

These criticisims certainly have some validity, and indicate that caution needs to be taken when analysing and interpreting phylogenies based on weighted trees. Weighted trees should never be used to develop a classification; consensus trees provide the most conservative estimate of phylogenetic relationships, and it is these that classifications should be developed from.

The value and use of a posteriori character weighting is to converge on fewer trees and to develop alternative phylogenetic hypotheses to those represented by strict consensus trees. The application of weighting methods is appropriate in the well supported *Carmichaelia* complex where there are a number of weakly supported branches. For example, that the *Carmichaelia* complex is well supported is indicated by the high bootstrap value (Fig. 6.10) and the strict consensus trees of several different analyses of the same data set (Fig. 6.9, 6.10, 6.11A, 6.11B, 6.11C), but the internal

species and species group relationships are often poorly resolved or weakly supported, as is evidenced by several polytomies and some bootstrap values below 50%. Character weighting has improved the resolution of the phylogenetic hypotheses, and this has advanced their usefulness in that they can be tested against other data, such as a species ecological preferences or distributions. The effectiveness of character weighting in developing better resolved phylogenetic hypotheses is well illustrated by comparing Fig. 6.9 with Fig. 6.10, and Fig. 6.11C with Fig. 6.11D.

Table 6.1 Major characters shared in different combinations among species of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium*.

Character	*Ca. kirkii*	*Ca. monroi*	*Ca. odorata*	*Ca. compacta*	*Ch. muritai*	*Ch. stevensonii*	*Co. crassicaule*	*N. glabrescens*
Habit-heteroblasty	present - spreading	absent	present - spreading	present - spreading	present - ascending	present - ascending	present - ascending	present - ascending
Stem grooving	absent	absent	absent	absent	present	present	present	absent
Phloem stone cells	absent	absent	present	absent	present	present	present	present
Ray parenchyma cells	heterogeneous	heterogeneous	heterogeneous	heterogeneous	homogeneous	homogeneous	heterogeneous	homogeneous
Leaf type	compound	unifoliolate	compound	compound	unifoliolate	unifoliolate	unifoliolate, compound	unifoliolate
Leaf-heteroblasty	absent	absent	absent	absent	present	present	present	present
Style hairs	present	present	absent	absent	absent	present	present	present
Anther	unilocular	unilocular	unilocular	unilocular	bilocular	bilocular	bilocular	bilocular
Keel length	> 6 mm	> 6 mm	< 6 mm	< 6 mm	< 6 mm	> 6 mm	> 6 mm	> 6 mm
Wing v's keel length	W < K	W < K	W > K	W > K	W > K	W < K	W < K	W < K
Fruit (in)dehiscent	dehiscent	indehiscent	dehiscent	indehiscent	indehiscent	indehiscent	indehiscent	indehiscent
Fruit hairs	absent	absent	absent	absent	present	present	present	absent
Radicle folding	folded	not folded	not folded	not folded	folded	folded	folded	folded

CHAPTER SEVEN

CONCLUSIONS AND SUMMARY

7.1 CONCLUSIONS

Chapter 1 outlined two main objectives for this thesis. These were to provide a stable and reliable species level classification for the genera *Carmichaelia* and *Notospartium*, and to develop a phylogenetic hypothesis for *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* that would enable the relationships of the four genera to be assessed. Two minor objectives were to investigate the evolutionary ecology of the *Carmichaelia* complex using wood anatomical data and heteroblastism characters.

This thesis has been successful in achieving the two main goals of providing a stable species level classification in *Carmichaelia* and *Notospartium*, and in developing a robust phylogenetic hypothesis.

The taxonomic revision of *Carmichaelia* significantly reduced the number of endemic New Zealand species from 38 to 17. The recognition of only 17 species resulted from giving increased emphasis to floral characters which had been overlooked in previous revisions, and placing less emphasis on pod and branchlet size and shape. The revision of *Carmichaelia* is based on traditional techniques such as the study of herbarium specimens, field observations and collections, and the cultivation of plants under uniform garden conditions. The application of the morphological species concept generally worked very well in regard to floral characters in *Carmichaelia.* However, in some species, for example *C. australis*, it has been necessary to accept variation in pod and branchlet characters throughout the range of the species. This variation may count against the successful application of the morphological species concept, but such variation is acceptable and can be attributed to natural variation among populations that are otherwise united by uniform floral characters. The new and revised taxonomy of *Carmichaelia* is considered to provide a pragmatic and functional classification, and in this regard it answers the concerns that have been raised about the difficulties of identifying species of *Carmichaelia* by Hooker (1864), Kirk (1899), Cheeseman (1906), Purdie (1984), and Wilson & Galloway (1993).

The phylogenetic analysis proved to be particularly useful to develop phylogenetic hypotheses for species and generic level relationships. The strengths of this analysis are that it is objective and repeatable, and that it has provided explicit hypotheses that allow for the critical evaluation and assessment of the generic level taxonomy of the group. A limitation of the phylogenetic analyses presented here is that species relationships vary depending on the parameters used for the analysis. For example, the exclusion or inclusion of the quantitative characters altered relationships, and the random searches identified two islands of trees, each with a different topology.

The phylogenetic analysis provided a framework for examining character evolution and distribution, and in particular the relationship between characters and generic boundaries. The main taxonomic outcome of the phylogenetic study is that the generic boundaries of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* are misplaced, and it is recommended that *Carmichaelia* be recircumscribed to include the other segregate genera. This outcome provides a positive answer to the concerns that have been raised by many earlier authors (Hooker 1957; Armstrong 1881; Cheeseman 1911, 1925; Slade 1952, 1953) about the recognition of the genera *Chordospartium*, *Corallospartium*, and *Notospartium*, and their relationship to each other and *Carmichaelia*.

7.2 SUMMARY

The results and conclusions drawn from Chapters 2, 3, 4, 5, and 6 are summarised below. The first two headings outline the results of the typification and taxonomic revision. This is followed by a summary of the major conclusions derived from the wood anatomy, heteroblasty, and phylogenetic parts of the study.

Typification

Typification was completed for 68 names in *Carmichaelia*, 2 in *Chordospartium*, 1 in *Corallospartium*, and 3 in *Notospartium*. Many names had to be lectotypified as the original collection on which a name was based would often include plant material collected from different localities, on different dates, by different collectors, and occasionally also included plant material subsequently assigned to different taxa.

Names in *Carmichaelia* that had been published by George Simpson needed special treatment as Simpson had a particular method of collecting type plant material. Simpson's concept of type material was broad and included plant material from the wild, and also cultivated material that was propagated from the original wild collection but which was pressed at a later date.

Taxonomy of *Carmichaelia* and *Notospartium*

In *Carmichaelia* 17 species are recognised. This number is a significant reduction from the 38 species names and 8 varietal names accepted by Allan (1961). There are several significant name changes including *C. arborea* being the earliest name for plants previously known as *C. grandiflora*, *C. australis* being the earliest name for the widespread and shrubby broom, *C. nana* replacing *C. enysii*, and *C. juncea* being reinstated and including *C. fieldii*, *C. prona*, *C. lacustris*, and *C. nigrans*.

Considerable intraspecific variation is accepted as occurring in the widespread *C. australis*, *C. corrugata*, *C. nana*, *C. odorata*, and *C. petriei*. As an indication of the variation each of these names includes several synonyms. *Carmichaelia australis* is the most widespread species occurring throughout the North Island and most of the South Island, and it has 25 synonyms. It exhibits clinal and geographic variation in stem width and shape, seed colour, and pod size and shape.

Notospartium includes three species, two of which are endemic to Marlborough. *Notospartium glabrescens* and *N. carmichaeliae* are distinguished by the size and shape of their pods and they are allopatric, growing on riparian bluffs, cliffs, and alluvium in eastern and western Marlborough respectively. They are separated by the Awatere Fault, which runs parallel to the Awatere River. *Notospartium glabrescens* is a calcicole, growing on soils derived from base-rich limestone, sandstone, mudstone, and siltstone parent materials. *Notospartium carmichaeliae* occurs on well-indurated greywackes of the Torlesse Supergroup which are base-poor.

Wood anatomy

The wood anatomy of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* is consistent with their placement in the Fabaceae subfamily Faboideae.

These species share with the majority of the woody Fabaceae diffuse porus wood, vessels with simple perforation plates, vestured alternate intervessel pitting, and vessel-ray pitting of the same size.

Wood anatomy of *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* is characterised by vessels with helical thickening and simple perforations; vessels, axial parenchyma, and short rays arranged in storied structure; predominantly fusiform parenchyma; and rays 1-20 cells wide. The ray cells of *Carmichaelia* and *Corallospartium* are procumbent, square, or upright, and those of *Chordospartium* and *Notospartium* procumbent.

The wood of the *Carmichaelia* complex has well developed xeromorphic features that include narrow diameter and short vessel elements, high numbers of vessels per mm^2, and the vessels usually arranged in pronounced diagonal aggregations. Vulnerability and mesomorphy indices are calculated and these support the relationship between species wood anatomy and the xeric habitats they occupy.

Heteroblasty

Habit-heteroblasty occurs in *Chordospartium*, *Corallospartium*, and *Notospartium*, and most species of *Carmichaelia*. Transition from the juvenile to the adult occurs in the first year after seed germination, and is marked by an abrupt change in stem habit and morphology and in leafiness. *Carmichaelia astonii*, *C. monroi*, *C. nana*, and *C. williamsii* pass from the juvenile to the adult without change.

Leaf-heteroblasty occurs in *Chordospartium*, *Corallospartium*, and *Notospartium*, whereas the leaves of *Carmichaelia* are usually of similar shape on juvenile and adult plants.

The orientation of the juvenile stems can be correlated with ecological preferences. Species with upright stems favour shaded habitats, whereas those with decumbent or prostrate stems prefer open habitats.

Phylogenetic analysis

A phylogenetic analysis of *Carmichaelia*, *Chordospartium*, *Corallospartium*,

Notospartium, *Clianthus*, and *Swainsona* resulted in two islands of equally parsimonious trees of 175 steps. Strict consensus trees identify a monophyletic New Zealand clade and a monophyletic Australian clade, and the phylogenetic analysis implies a single dispersal event to New Zealand.

The taxa in the New Zealand clade are characterised by being woody shrubs or dwarf shrubs, having terminal innovation shoots, persistent pith, wide ray parenchyma, vessel elements with helical thickenings, and slender and flexuose phloem fibres.

Carmichaelia is paraphyletic if *Chordospartium*, *Corallospartium*, and *Notospartium* are excluded. The patterns of character distribution and species relationships indicate that no group of characters adequately circumscribes any of the four genera. A single character will often distinguish a particular group of species, genus, or genera, but this will be contradicted by other characters of equal taxonomic significance that define different taxonomic assemblages and that frequently cut across the four genera. Recommendations are made for a recircumscription of Carmichaelia to include *Chordospartium*, *Corallospartium*, and *Notospartium*.

Swainsona is paraphyletic if *S. novae-zelandiae* is included with Australian species of *Swainsona*. It is recommended that *Swainsona novae-zelandiae* be segregated from *Swainsona* and placed into a new monotypic genus.

An analysis of character distribution and variation indicates that *Ch. muritai* may have a hybrid origin. This species shares bilocular anthers with *Ch. stevensonii*, *Corallospartium*, and *Notospartium*, it has a similar fruit to *Ch. stevensonii* and *Corallospartium*, but it has in common with several species of *Carmichaelia* (e.g., *Ca. australis*) a glabrous style, a small keel, and wings being longer than the keel.

The inclusion of five quantitative characters and reweighting of all characters by the rescaled consistency index assisted in resolving polytomies within the *Carmichaelia* clade.

7.3 FUTURE RESEARCH

The taxonomy of prostrate forms of *Carmichaelia* in the Canterbury region needs to be investigated. Two indeterminate forms of prostrate *Carmichaelia* occur, one in the upper Rangitata River catchment and the other on the coastal cliffs between the Rakaia and Rangitata Rivers. In both areas the prostrate forms are sympatric with upright *C.*

australis, and the relationship of these forms to *C. appressa* needs to be investigated, possibly with allozymes.

The taxonomic status of the slender and few-flowered *Corallospartium crassicaule* var. *racemosum* also needs to be investigated. This form seems to be allopatric with *C. crassicaule* and occurs in Otago from near Lindis Pass to Lake Wakatipu. The distribution of the taxon does not appear to be correlated with any geological or soil characteristics.

There are also a large number of threatened species in the *Carmichaelia* complex. The ecology of the threatened and some of the widespread and common species should be compared to see if there are any ecological or environmental factors that restrict distributions and influence rarity. For some rare species establishing the level of inter- and intra-population genetic variation would be important information to assist with establishing conservation priorities. *Carmichaelia juncea* is one species that would benefit from such a study.

The development of a molecular phylogenetic hypothesis would be useful for several reasons. It would allow comparison and assessment of congruence with the anatomical/morphological phylogeny and it would facilitate studies of character evolution and adaptive radiation. In addition, it would allow for an independent appraisal of the taxonomy of the group.

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APPENDICES

Appendix 1. Raw data for the statistical analysis of stem and pod variation in *Carmichaelia australis* (Chapter 3). Lake Lyndon population at NZMS 260 K35 045 664; Dry Stream population at NZMS 260 K34 058 713; Coleridge population at NZMS 260 K35 965 618; Lyndon Road population at NZMS 260 K35 025 632; Rakaia River population at NZMS 260 K35 945 536; Akaroa population at NZMS 260 N37 058 082; Lake Forsyth population at NZMS 260 M36 885 118; Mt Cavendish population at NZMS 260 M36 869 356; Ellesmere population at NZMS 260 M36 795 167; Taumarunui population at NZMS 260 S18 06- 55-; Manawatu population at NZMS 260 T24 47- 96-; Tongariro population at NZMS 260 T19 31- 26-; Egmont population at NZMS 260 P20 04-15-.

Population	Plant	Code	Stem	Pod length	Pod width
Lake Lyndon	1	aa	2.96	7.93	3.51
Lake Lyndon	1	aa	2.95	9.94	3.87
Lake Lyndon	1	aa	2.65	9.53	3.94
Lake Lyndon	1	aa	2.83	9.22	3.75
Lake Lyndon	1	aa	3	9.43	3.73
Lake Lyndon	2	ab	3.14	9.06	3.51
Lake Lyndon	2	ab	3.2	7.75	3.37
Lake Lyndon	2	ab	2.21	8.43	3.26
Lake Lyndon	2	ab	2.69	8.35	3.64
Lake Lyndon	2	ab	2.38	7.28	3.28
Lake Lyndon	3	ac	2.36	7.87	3.41
Lake Lyndon	3	ac	2.69	7.98	4.12
Lake Lyndon	3	ac	3.38	9.38	4.25
Lake Lyndon	3	ac	2.29	8.61	3.38
Lake Lyndon	3	ac	2.93	9.02	4.15
Lake Lyndon	4	ad	3.13	10.06	3.7
Lake Lyndon	4	ad	2.74	8.62	3.25
Lake Lyndon	4	ad	2.91	7.9	3.25
Lake Lyndon	4	ad	2.43	8.16	2.76
Lake Lyndon	4	ad	3.28	7.53	3.18
Lake Lyndon	5	ae	2.83	7.72	3.48
Lake Lyndon	5	ae	2.86	9.32	3.56
Lake Lyndon	5	ae	2.8	8.82	3.04
Lake Lyndon	5	ae	2.92	8.58	3.82
Lake Lyndon	5	ae	2.98	8.13	3.47
Lake Lyndon	6	af	2.33	7.43	3
Lake Lyndon	6	af	2.38	7.72	2.65
Lake Lyndon	6	af	2.36	7.71	2.43
Lake Lyndon	6	af	2.61	7.55	2.78
Lake Lyndon	6	af	2.63	7.28	2.91
Lake Lyndon	7	ag	2.25	7.41	2.92
Lake Lyndon	7	ag	2.45	6.53	2.36
Lake Lyndon	7	ag	3	7.6	2.65
Lake Lyndon	7	ag	2.92	6.81	2.58
Lake Lyndon	7	ag	2.35	7.82	2.79

Dry Stream	1	ah	3.43	5.63	2.82
Dry Stream	1	ah	2.84	6.78	2.87
Dry Stream	1	ah	2.66	5.45	2.62
Dry Stream	1	ah	2.81	6.97	2.97
Dry Stream	1	ah	2.69	7.03	2.69
Dry Stream	2	ai	3.8	8.62	2.87
Dry Stream	2	ai	3.36	8.51	3.15
Dry Stream	2	ai	3.84	7.59	2.94
Dry Stream	2	ai	3.33	8.8	2.89
Dry Stream	2	ai	3.63	8.69	2.88
Dry Stream	3	aj	3.45	9.77	3.35
Dry Stream	3	aj	3.72	8.42	3.13
Dry Stream	3	aj	4.09	9	3.17
Dry Stream	3	aj	3.74	8.77	2.77
Dry Stream	3	aj	3.87	8.65	3.11
Dry Stream	4	ak	3.05	8.58	3.18
Dry Stream	4	ak	2.74	7.13	2.58
Dry Stream	4	ak	2.28	9.45	3.16
Dry Stream	4	ak	2.12	7.41	3.08
Dry Stream	4	ak	3.2	8.79	3.21
Dry Stream	5	al	2.65	10:33	4.15
Dry Stream	5	al	2.13	11.91	3.79
Dry Stream	5	al	2.22	10.26	3.52
Dry Stream	5	al	2.58	11.11	3.5
Dry Stream	5	al	2.83	10.15	3.34
Dry Stream	6	am	3.58	6.62	2.76
Dry Stream	6	am	3.24	6.61	2.84
Dry Stream	6	am	2.94	6.88	2.86
Dry Stream	6	am	3.25	5.67	2.77
Dry Stream	6	am	3.21	6.99	2.84
Dry Stream	7	an	2.69	6.13	3.12
Dry Stream	7	an	2.89	6.45	3.54
Dry Stream	7	an	3.01	6.98	3.19
Dry Stream	7	an	2.19	6.81	2.64
Dry Stream	7	an	3	8.49	3.28
Dry Stream	8	ao	2.45	6.81	2.75
Dry Stream	8	ao	2.59	7.44	3.18
Dry Stream	8	ao	2.81	6.74	2.73
Dry Stream	8	ao	2.76	6.73	2.65
Dry Stream	8	ao	2.48	8.09	3.01
Dry Stream	9	ap	2.54	8.91	2.95
Dry Stream	9	ap	2.1	7.34	3.09
Dry Stream	9	ap	2.9	9.73	3.06
Dry Stream	9	ap	2.96	10.63	3.8
Dry Stream	9	ap	2.05	8.78	3.14
Dry Stream	10	aq	3.1	8.59	2.92
Dry Stream	10	aq	2.97	7.22	2.46
Dry Stream	10	aq	3.27	7.64	2.71
Dry Stream	10	aq	3.02	8.62	2.89

Dry Stream	10	aq	2.76	7.99	2.96
Dry Stream	11	ar	2.86	8.23	3.24
Dry Stream	11	ar	2.4	7.5	3.14
Dry Stream	11	ar	3.03	7.07	3.36
Dry Stream	11	ar	3.28	7.29	3.13
Dry Stream	11	ar	3.52	8.24	3.32
Dry Stream	12	as	3.5	6.37	2.15
Dry Stream	12	as	2.75	7.26	2.56
Dry Stream	12	as	3.24	7.43	3.02
Dry Stream	12	as	3.36	7.75	2.55
Dry Stream	12	as	2.96	7.73	3.02
Dry Stream	13	at	2.93	10.49	3.69
Dry Stream	13	at	2.36	11.63	3.66
Dry Stream	13	at	2.28	10.86	3.39
Dry Stream	13	at	2.62	10.87	3.21
Dry Stream	13	at	2.75	10.27	3.78
Dry Stream	14	au	2.75	6.56	3.04
Dry Stream	14	au	2.69	6.78	2.47
Dry Stream	14	au	3.09	6.79	2.37
Dry Stream	14	au	2.98	6.44	2.36
Dry Stream	14	au	2.94	6.92	2.65
Dry Stream	15	av	3.15	9.05	3.2
Dry Stream	15	av	2.71	9.14	2.96
Dry Stream	15	av	2.26	8.8	2.98
Dry Stream	15	av	2.67	7.11	2.65
Dry Stream	15	av	2.56	9	3.07
Dry Stream	16	aw	2.65	8.1	2.9
Dry Stream	16	aw	2.34	8.69	3.4
Dry Stream	16	aw	2.53	6.55	2.26
Dry Stream	16	aw	2.54	6.97	2.65
Dry Stream	16	aw	2.66	7.78	2.94
Dry Stream	17	ax	3.04	5.78	3.05
Dry Stream	17	ax	3.65	5.16	3.12
Dry Stream	17	ax	2.8	5.62	3.42
Dry Stream	17	ax	3.18	6.4	3.67
Dry Stream	17	ax	2.86	6.88	3.46
Dry Stream	18	ay	2.6	7.99	2.97
Dry Stream	18	ay	2.59	8.63	2.93
Dry Stream	18	ay	2.51	6.89	2.7
Dry Stream	18	ay	2.69	7.45	3.45
Dry Stream	18	ay	2.89	6.86	3.07
Dry Stream	19	az	2.95	9.82	2.85
Dry Stream	19	az	3	6.25	2.5
Dry Stream	19	az	2.43	7.65	2.46
Dry Stream	19	az	2.33	6.49	2.86
Dry Stream	19	az	2.53	8.64	2.84
Dry Stream	20	ba	2.25	9.57	3.19
Dry Stream	20	ba	2.25	9.57	3.1
Dry Stream	20	ba	2.58	9.52	3.01

Dry Stream	20	ba	2.37	9.43	2.87
Dry Stream	20	ba	1.87	9.63	2.93
Dry Stream	21	bb	3.39	7.63	3.02
Dry Stream	21	bb	2.98	7.63	3.13
Dry Stream	21	bb	3.1	6.51	2.75
Dry Stream	21	bb	3.25	6.76	2.56
Dry Stream	21	bb	2.72	7.95	3.35
Dry Stream	22	bc	3.2	7.07	2.74
Dry Stream	22	bc	3.24	8.56	2.74
Dry Stream	22	bc	2.4	9.49	2.75
Dry Stream	22	bc	3.23	8.65	2.66
Dry Stream	22	bc	3.31	9.02	2.52
Dry Stream	23	bd	2.76	7.65	2.85
Dry Stream	23	bd	3.25	8.01	2.86
Dry Stream	23	bd	2.36	7.04	2.61
Dry Stream	23	bd	2.54	7.34	2.57
Dry Stream	23	bd	2.69	7.06	2.55
Dry Stream	24	be	2.85	8.22	3.12
Dry Stream	24	be	2.39	7.7	2.82
Dry Stream	24	be	3.21	8.95	3.1
Dry Stream	24	be	3.45	8.72	2.73
Dry Stream	24	be	2.47	7.36	2.42
Dry Stream	25	bf	3.94	8.94	2.76
Dry Stream	25	bf	4	9.62	3.1
Dry Stream	25	bf	3.25	9.75	2.87
Dry Stream	25	bf	3.3	10.79	2.96
Dry Stream	25	bf	3.24	9.2	2.59
Dry Stream	26	bg	2.5	7.69	2.48
Dry Stream	26	bg	2.1	7	2.76
Dry Stream	26	bg	2.6	6.92	2.3
Dry Stream	26	bg	2.67	7.55	2.6
Dry Stream	26	bg	2.6	6.77	2.4
Coleridge	1	bh	3.33	9.22	2.87
Coleridge	1	bh	3.16	10.9	3.39
Coleridge	1	bh	3.51	10.85	3.14
Coleridge	1	bh	3.22	9.5	3.65
Coleridge	1	bh	2.87	10.63	2.96
Coleridge	2	bi	3.3	9.22	2.99
Coleridge	2	bi	3.08	9.64	2.71
Coleridge	2	bi	3.66	8.65	3.06
Coleridge	2	bi	3.32	8.66	3
Coleridge	2	bi	3.19	9.29	2.9
Coleridge	3	bj	2.26	10.56	2.46
Coleridge	3	bj	2.85	8.29	2.38
Coleridge	3	bj	2.63	10.16	2.8
Coleridge	3	bj	2.51	9.28	2.75
Coleridge	3	bj	3.41	9.89	2.72
Coleridge	4	bk	2.54	11.87	3.5
Coleridge	4	bk	2.21	10.43	3.5

Coleridge	4	bk	2.34	10.36	3.33
Coleridge	4	bk	2.69	12.36	3.45
Coleridge	4	bk	2.35	10.72	3.26
Coleridge	5	bl	2.24	9.56	2.95
Coleridge	5	bl	2.41	9.12	2.82
Coleridge	5	bl	2.77	9.92	2.72
Coleridge	5	bl	2.67	9.64	3.07
Coleridge	5	bl	2.47	9.21	2.93
Coleridge	6	bm	2.94	7.38	3.63
Coleridge	6	bm	2.29	8.15	3.38
Coleridge	6	bm	2.2	7.5	3.09
Coleridge	6	bm	2.18	7.87	3.21
Coleridge	6	bm	2.58	7.58	3.35
Coleridge	7	bn	3.08	10.03	2.94
Coleridge	7	bn	2.94	10.7	2.7
Coleridge	7	bn	3.03	9.63	2.7
Coleridge	7	bn	2.47	10.09	2.8
Coleridge	7	bn	2.47	9.8	2.85
Coleridge	8	bo	1.95	8.32	2.61
Coleridge	8	bo	2.78	8.49	2.93
Coleridge	8	bo	2.84	7.82	2.59
Coleridge	8	bo	2.33	8.06	2.66
Coleridge	8	bo	2.24	7.48	2.66
Coleridge	9	bp	2.2	6.63	3.13
Coleridge	9	bp	2.47	6.34	2.19
Coleridge	9	bp	2.8	6.79	2.54
Coleridge	9	bp	2.95	7.25	3.06
Coleridge	9	bp	3.15	6.78	3.23
Coleridge	10	bq	2.34	7.71	3.05
Coleridge	10	bq	2.31	6.9	2.81
Coleridge	10	bq	1.89	7.35	2.98
Coleridge	10	bq	2.45	7.84	3.12
Coleridge	10	bq	2.2	8.15	3.16
Coleridge	11	br	2.48	8.41	2.69
Coleridge	11	br	3.29	8.25	2.59
Coleridge	11	br	2.92	8.04	2.75
Coleridge	11	br	2.5	8.26	2.43
Coleridge	11	br	2.29	7.78	2.51
Coleridge	12	bs	3.49	7.6	2.36
Coleridge	12	bs	3.07	6.74	2.7
Coleridge	12	bs	3.24	6.96	2.7
Coleridge	12	bs	3.21	7.26	2.64
Coleridge	12	bs	2.88	6.13	2.57
Coleridge	13	bt	3.11	9.04	2.91
Coleridge	13	bt	3.76	8.13	2.49
Coleridge	13	bt	2.94	6.98	2.77
Coleridge	13	bt	2.96	8.03	2.47
Coleridge	13	bt	2.66	7.68	2.45
Coleridge	14	bu	2.48	7.94	2.97

Coleridge	14	bu	2.4	7.43	2.89
Coleridge	14	bu	2.46	7.95	3.07
Coleridge	14	bu	2.08	8.36	3.16
Coleridge	14	bu	2.93	7.74	2.96
Coleridge	15	bv	2.7	6.11	2.5
Coleridge	15	bv	3.03	6.72	3.05
Coleridge	15	bv	2.22	6.36	2.77
Coleridge	15	bv	2.1	6.38	2.57
Coleridge	15	bv	2.28	6.65	2.83
Coleridge	16	bw	2.61	6.28	2.6
Coleridge	16	bw	3.27	6.8	2.87
Coleridge	16	bw	3.2	6.37	2.6
Coleridge	16	bw	3.17	6.89	2.74
Coleridge	16	bw	3.29	7.27	3.11
Coleridge	17	bx	2.89	6.12	2.61
Coleridge	17	bx	2.48	7.26	2.7
Coleridge	17	bx	2.6	6.94	2.79
Coleridge	17	bx	3.04	5.2	2.14
Coleridge	17	bx	3.3	7.84	2.95
Coleridge	18	by	2.38	6.85	2.58
Coleridge	18	by	2.45	6.53	2.89
Coleridge	18	by	2.63	6.4	2.68
Coleridge	18	by	2.61	6.17	2.28
Coleridge	18	by	2.95	6.04	2.46
Coleridge	19	bz	3.21	7.52	2.97
Coleridge	19	bz	3.13	7.72	3.16
Coleridge	19	bz	3.26	6.69	3.17
Coleridge	19	bz	3.1	6.83	2.84
Coleridge	19	bz	3.12	7.14	2.89
Coleridge	20	ca	2.33	6.95	2.67
Coleridge	20	ca	3.11	7.19	2.75
Coleridge	20	ca	2.96	7.45	2.69
Coleridge	20	ca	2.41	6.58	2.53
Coleridge	20	ca	2.58	6.85	2.41
Coleridge	21	cb	2.56	7.68	2.65
Coleridge	21	cb	2.51	6.95	2.47
Coleridge	21	cb	3.28	7.05	2.41
Coleridge	21	cb	3.31	4.98	2.21
Coleridge	21	cb	2.12	5.57	2.32
Coleridge	22	cc	2.56	7.62	2.9
Coleridge	22	cc	3.08	7.94	3.21
Coleridge	22	cc	2.42	8.09	3.21
Coleridge	22	cc	2.14	7.44	3.27
Coleridge	22	cc	3.31	6.68	2.87
Coleridge	23	cd	2.37	8.44	2.86
Coleridge	23	cd	2.57	8.73	2.77
Coleridge	23	cd	2.63	7.53	2.65
Coleridge	23	cd	2.68	8.13	2.93
Coleridge	23	cd	3.08	6.83	2.49

Coleridge	24	ce	2.16	8.49	3.06
Coleridge	24	ce	1.9	8.49	2.9
Coleridge	24	ce	2.78	7.24	2.58
Coleridge	24	ce	2.06	7.25	2.86
Coleridge	24	ce	2.4	7.75	3.03
Lyndon Road	1	cf	3.27	8.41	3.04
Lyndon Road	1	cf	4.74	9.11	3.09
Lyndon Road	1	cf	4.97	8.15	3.05
Lyndon Road	1	cf	3.99	8.15	3.1
Lyndon Road	1	cf	4.41	9.01	3.24
Lyndon Road	2	cg	2.71	6.06	3.4
Lyndon Road	2	cg	2.67	4.81	2.8
Lyndon Road	2	cg	2.65	5.3	3.27
Lyndon Road	2	cg	2.43	5.1	3.18
Lyndon Road	2	cg	2.9	5.36	3.07
Lyndon Road	3	ch	2.6	8.31	3.02
Lyndon Road	3	ch	2.7	6.95	2.62
Lyndon Road	3	ch	2.63	7.22	3.21
Lyndon Road	3	ch	3.02	8.42	3.2
Lyndon Road	3	ch	2.79	8.14	3.08
Lyndon Road	4	ci	2.78	5.98	2.85
Lyndon Road	4	ci	2.33	5.52	2.6
Lyndon Road	4	ci	2.55	5.98	2.68
Lyndon Road	4	ci	2.28	5.98	2.65
Lyndon Road	4	ci	2.32	6.19	3.05
Lyndon Road	5	cj	2.51	5.78	3.03
Lyndon Road	5	cj	2.86	7.33	3.53
Lyndon Road	5	cj	2.66	6.78	3.14
Lyndon Road	5	cj	2.49		
Lyndon Road	5	cj	2.75		
Lyndon Road	6	ck	2.33	9.8	3.58
Lyndon Road	6	ck	2.36	7.73	2.94
Lyndon Road	6	ck	2.61	9.99	3.32
Lyndon Road	6	ck	2.69	9.83	3.07
Lyndon Road	6	ck	2.17	9.83	3.26
Lyndon Road	7	cl	2.26	6	2.99
Lyndon Road	7	cl	2.17	7.09	2.99
Lyndon Road	7	cl	2.06	7.43	3.3
Lyndon Road	7	cl	1.86	7.93	3.27
Lyndon Road	7	cl	2.25	7.67	3.12
Lyndon Road	8	cm	3.35	8.3	3.04
Lyndon Road	8	cm	2.24	8.46	3.67
Lyndon Road	8	cm	2.49	7.85	3.23
Lyndon Road	8	cm	2.57	7.8	3.27
Lyndon Road	8	cm	2.5	8.13	3.55
Lyndon Road	9	cn	2.12	9.37	3.45
Lyndon Road	9	cn	1.99	8.14	3.28
Lyndon Road	9	cn	2.01	8.08	3.2
Lyndon Road	9	cn	2.52	10.45	3.3

Lyndon Road	9	cn	1.72	8.4	3.35
Lyndon Road	10	co	3.08	6.94	3.16
Lyndon Road	10	co	2.7	6.18	2.71
Lyndon Road	10	co	2.59	6.33	2.7
Lyndon Road	10	co	2.51	6.39	2.71
Lyndon Road	10	co	2.2	6.01	2.69
Lyndon Road	11	cp	2.59	6.48	2.35
Lyndon Road	11	cp	2.84	6.68	2.5
Lyndon Road	11	cp	3.29	7.26	2.76
Lyndon Road	11	cp	2.51	6.63	2.16
Lyndon Road	11	cp	3.01	6.6	2.79
Lyndon Road	12	cq	2.92	7.15	3.15
Lyndon Road	12	cq	3.6	6.77	3.66
Lyndon Road	12	cq	2.89	6.78	3.32
Lyndon Road	12	cq	3.14	7.62	3.57
Lyndon Road	12	cq	2.92	7.41	3.51
Lyndon Road	13	cr	3.16	7.52	3.12
Lyndon Road	13	cr	2.78	7.1	3.12
Lyndon Road	13	cr	3	7.2	2.94
Lyndon Road	13	cr	2.4	7.01	2.94
Lyndon Road	13	cr	2.63	6.76	2.96
Lyndon Road	14	cs	2.18	5.57	2.88
Lyndon Road	14	cs	2.74	7.05	3.15
Lyndon Road	14	cs	2.62	6.96	3.74
Lyndon Road	14	cs	2.67	7.62	3.17
Lyndon Road	14	cs	2.35	7.83	3.62
Lyndon Road	15	ct	3.07	7.52	3.18
Lyndon Road	15	ct	2.18	7.31	3.55
Lyndon Road	15	ct	2.75	7.44	3.23
Lyndon Road	15	ct	2.58	8.3	3.79
Lyndon Road	15	ct	2.41	8.27	3.43
Lyndon Road	16	cu	2.93	7.34	3.18
Lyndon Road	16	cu	3.32	7.43	3.26
Lyndon Road	16	cu	2.2	7.64	3.43
Lyndon Road	16	cu	2.47	7.64	3.48
Lyndon Road	16	cu	2.9	7.16	3.18
Lyndon Road	17	cv	2.07	8.66	2.79
Lyndon Road	17	cv	2.59	11.31	3.55
Lyndon Road	17	cv	2.23	10.82	3.38
Lyndon Road	17	cv	2.24	10.63	3.57
Lyndon Road	17	cv	2.08	9.57	3.27
Lyndon Road	18	cw	2.76	6.38	2.87
Lyndon Road	18	cw	2.89	7.32	3.02
Lyndon Road	18	cw	2.79	6.33	3.14
Lyndon Road	18	cw	3.3	6.12	2.67
Lyndon Road	18	cw	2.68	5.86	2.67
Lyndon Road	19	cx	2.79	8	3.42
Lyndon Road	19	cx	2.85	7.73	3.55
Lyndon Road	19	cx	2.62	6.8	3.12

Lyndon Road	19	cx	2.3	7.16	3.49
Lyndon Road	19	cx	2.56	7.01	3.24
Lyndon Road	20	cy	2.56	8.13	2.8
Lyndon Road	20	cy	2.33	7.97	3.9
Lyndon Road	20	cy	2.33	11.57	3.87
Lyndon Road	20	cy	2.05	9.33	4.07
Lyndon Road	20	cy	2.11	8.43	3.02
Lyndon Road	21	cz	2.34	6.62	2.68
Lyndon Road	21	cz	2.06	6.33	2.66
Lyndon Road	21	cz	2.13	5.27	2.62
Lyndon Road	21	cz	2.27	5.7	2.9
Lyndon Road	21	cz	2.52	6.58	2.71
Lyndon Road	22	da	2.81	9.2	2.75
Lyndon Road	22	da	2.19	8.89	2.74
Lyndon Road	22	da	2.62	8.67	2.74
Lyndon Road	22	da	2.19	8	2.74
Lyndon Road	22	da	2.33	7.09	2.59
Rakaia River	1	db	2.44	7.24	3.78
Rakaia River	1	db	2.34	6.46	3.53
Rakaia River	1	db	2.12	6.78	3.88
Rakaia River	1	db	2.89	6.38	3.7
Rakaia River	1	db	2.77	6.88	3.23
Rakaia River	2	dc	2.48	6.77	2.88
Rakaia River	2	dc	2.5	7.69	3.36
Rakaia River	2	dc	2.38	7.01	3.36
Rakaia River	2	dc	2.56	6.97	3.51
Rakaia River	2	dc	2.7	7	3.5
Rakaia River	3	dd	2.76	11.12	3.41
Rakaia River	3	dd	2.73	9.83	3.22
Rakaia River	3	dd	2.67	10.61	3.24
Rakaia River	3	dd	2.15	11.61	3.69
Rakaia River	3	dd	3.06	11.06	3.24
Rakaia River	4	de	1.86	6.81	3.86
Rakaia River	4	de	2.77	6.41	3.86
Rakaia River	4	de	2.37	6.42	3.75
Rakaia River	4	de	2.6	6.25	3.56
Rakaia River	4	de	2.23	6.27	3.23
Rakaia River	5	df	2.83	7.04	3.54
Rakaia River	5	df	2.97	8	3.54
Rakaia River	5	df	2.78	7.25	3.28
Rakaia River	5	df	3.27	7.7	3.41
Rakaia River	5	df	2.7	7.18	3.08
Rakaia River	6	dg	3.27	6.81	3.03
Rakaia River	6	dg	3.84	6.99	3.4
Rakaia River	6	dg	3.15	6.52	3.34
Rakaia River	6	dg	2.61	7.67	3.64
Rakaia River	6	dg	2.79	7.68	3.68
Rakaia River	7	dh	2.63	6.09	3.27
Rakaia River	7	dh	2.36	6.15	3.01

Rakaia River	7	dh	2.58	6.18	2.95
Rakaia River	7	dh	2.94	7.33	3.22
Rakaia River	7	dh	2.8	7.15	3.11
Rakaia River	8	di	2.25	5.3	3.35
Rakaia River	8	di	2.34	5.95	3.43
Rakaia River	8	di	2.2	5.43	3.16
Rakaia River	8	di	1.98	5.14	2.64
Rakaia River	8	di	1.57	4.97	2.71
Rakaia River	9	dj	2.86	6.2	2.8
Rakaia River	9	dj	2.58	6.86	2.99
Rakaia River	9	dj	3.08	5.9	2.69
Rakaia River	9	dj	2.44	6.57	2.84
Rakaia River	9	dj	2.64	6.37	2.55
Rakaia River	10	dk	2.34	7.65	4.4
Rakaia River	10	dk	2.91	6.9	4.46
Rakaia River	10	dk	2.61	6.79	3.98
Rakaia River	10	dk	2.59	7.79	4.17
Rakaia River	10	dk	3.03	7.67	4.18
Rakaia River	11	dl	2.38	10.32	3.76
Rakaia River	11	dl	2.45	8.45	2.97
Rakaia River	11	dl	2.24	9.44	3.75
Rakaia River	11	dl	2.36	10.88	3.8
Rakaia River	11	dl	2.43	9.64	3.71
Rakaia River	12	dm	2.67	7.38	3.5
Rakaia River	12	dm	2.8	7.96	3.2
Rakaia River	12	dm	2.21	6.34	2.67
Rakaia River	12	dm	2.63	7.81	3.4
Rakaia River	12	dm	2.23	8.12	3.65
Rakaia River	13	dn	2	7.58	3.11
Rakaia River	13	dn	1.99	9.89	3.65
Rakaia River	13	dn	1.89	10.31	3.7
Rakaia River	13	dn	1.83	9.85	3.69
Rakaia River	13	dn	1.75	8.59	3.47
Rakaia River	14	do	2.11	7.01	2.44
Rakaia River	14	do	1.99	7.05	3.01
Rakaia River	14	do	2.01	6.49	2.59
Rakaia River	14	do	1.88	7.32	2.92
Rakaia River	14	do	1.85	7.05	2.68
Rakaia River	15	dp	2.2	6.62	2.55
Rakaia River	15	dp	2.24	7.3	2.82
Rakaia River	15	dp	2.16	6.99	2.98
Rakaia River	15	dp	1.96	6.88	2.9
Rakaia River	15	dp	1.65	6.97	2.66
Rakaia River	16	dq	1.77	7.63	3.2
Rakaia River	16	dq	1.91	8.81	3.01
Rakaia River	16	dq	1.74	7.55	2.83
Rakaia River	16	dq	2.11	7.88	2.85
Rakaia River	16	dq	1.38	6.92	3.11
Rakaia River	17	dr	1.62	7.38	2.96

Rakaia River	17	dr	1.77	6.57	2.2
Rakaia River	17	dr	2.02	8.15	2.94
Rakaia River	17	dr	1.92	6.75	2.53
Rakaia River	17	dr	1.87	7.26	2.78
Rakaia River	18	ds	2.62	9.41	3.64
Rakaia River	18	ds	2.14	12.02	4.02
Rakaia River	18	ds	2.16	8.88	3.65
Rakaia River	18	ds	1.82	9.59	3.95
Rakaia River	18	ds	2.78	9.81	3.53
Rakaia River	19	dt	2.35	7.03	4.27
Rakaia River	19	dt	2.08	9.33	3.74
Rakaia River	19	dt	2.49	9.08	3.78
Rakaia River	19	dt	2.39	8.23	3.57
Rakaia River	19	dt	2.42	6.78	3
Rakaia River	20	du	3.03	9.21	3.9
Rakaia River	20	du	2.47	8.99	3.8
Rakaia River	20	du	2.14	8.58	3.78
Rakaia River	20	du	2.52	7.76	3.19
Rakaia River	20	du	2.71	8.62	3.36
Rakaia River	21	dv	2.4	8.04	2.73
Rakaia River	21	dv	2.52	8.7	3.04
Rakaia River	21	dv	2.56	8.81	2.95
Rakaia River	21	dv	2.61	8.29	3.13
Rakaia River	21	dv	2.15	8.87	2.84
Rakaia River	22	dw	1.77	5.7	2.48
Rakaia River	22	dw	1.75	5.28	2.48
Rakaia River	22	dw	1.77	7.55	2.73
Rakaia River	22	dw	1.85	7.85	2.89
Rakaia River	22	dw	1.67	7.13	2.56
Rakaia River	23	dx	2.5	8.26	2.7
Rakaia River	23	dx	1.99	8.45	2.82
Rakaia River	23	dx	1.93	9.64	3.19
Rakaia River	23	dx	1.86	10.83	2.67
Rakaia River	23	dx	2.16	9.4	2.7
Rakaia River	24	dy	3.41	7.44	3.68
Rakaia River	24	dy	2.96	7.15	3.69
Rakaia River	24	dy	2.58	7.57	3.53
Rakaia River	24	dy	2.53	7.07	3.43
Rakaia River	24	dy	2.95	8.14	4.03
Rakaia River	25	dz	3.08	8.74	3.26
Rakaia River	25	dz	3.01	9.74	3.91
Rakaia River	25	dz	2.96	8.75	4.05
Rakaia River	25	dz	3.19	8.64	4.17
Rakaia River	25	dz	2.79	8.87	4.13
Rakaia River	26	ea	1.49	6.34	3.24
Rakaia River	26	ea	2.22	7.67	3.74
Rakaia River	26	ea	2.26	8.14	4.23
Rakaia River	26	ea	1.81	6.69	3.14
Rakaia River	26	ea	1.97	7.4	3.3

Rakaia River	27	eb	2.8	8.39	3.52
Rakaia River	27	eb	2.7	8.1	3.18
Rakaia River	27	eb	3.75	8.1	3.73
Rakaia River	27	eb	3.4	8.19	3.4
Rakaia River	27	eb	3.34	7.66	3.59
Rakaia River	28	ec	2.25	6.13	3.47
Rakaia River	28	ec	2.44	7.1	3.47
Rakaia River	28	ec	2.54	6.96	3.49
Rakaia River	28	ec	2.28	7.63	3.73
Rakaia River	28	ec	1.93	7.16	3.95
Rakaia River	29	ed	2.2	7.43	3.37
Rakaia River	29	ed	2.25	6.84	2.92
Rakaia River	29	ed	2.66	8	3.51
Rakaia River	29	ed	3	7.55	2.93
Rakaia River	29	ed	2.69	8.55	3.65
Rakaia River	30	ef	2.52	7.05	3.47
Rakaia River	30	ef	2.2	7.49	3.69
Rakaia River	30	ef	2.82	7.97	3.92
Rakaia River	30	ef	2.51	9.14	3.85
Rakaia River	30	ef	2.24	7.81	3.68
Akaroa	1	eg	1.02	6.3	2.53
Akaroa	1	eg	0.88	5.18	2.88
Akaroa	1	eg	1.26	5.95	2.77
Akaroa	1	eg	1.22	5.58	2.76
Akaroa	1	eg	1.14	5.81	2.95
Akaroa	2	eh	1.17	5.4	2.23
Akaroa	2	eh	1.03	4.88	2.39
Akaroa	2	eh	1.09	5.76	2.54
Akaroa	2	eh	0.88	4.39	2.39
Akaroa	2	eh	1.28	5.34	2.56
Akaroa	3	ei	1.25	4.8	2.7
Akaroa	3	ei	1.38	5.39	2.22
Akaroa	3	ei	1.64	5.76	2.72
Akaroa	3	ei	1.42	5.47	2.89
Akaroa	3	ei	1.4	4.56	2.84
Akaroa	4	ej	1.13	5.21	2.46
Akaroa	4	ej	1.05	4.12	2.35
Akaroa	4	ej	1	5.17	2.51
Akaroa	4	ej	1.27	4.41	2.62
Akaroa	4	ej	1.24	4.56	2.28
Akaroa	5	ek	1.31	5.35	3.23
Akaroa	5	ek	1.24	5.29	2.81
Akaroa	5	ek	1.23	6	3
Akaroa	5	ek	1.42	5.3	2.88
Akaroa	5	ek	1.88	4.2	2.38
Akaroa	6	el	1.04	4.8	2.73
Akaroa	6	el	0.95	4.35	2.53
Akaroa	6	el	1.02	4.93	2.2
Akaroa	6	el	1	4.72	2.72

Akaroa	6	el	0.98	4.82	2.61
Akaroa	7	em	1.2	5.81	2.8
Akaroa	7	em	0.95	6.31	2.63
Akaroa	7	em	0.88	6.01	2.66
Akaroa	7	em	1.06	6.01	2.8
Akaroa	7	em	1.34	5.73	2.62
Akaroa	8	en	1.28	4.67	2.83
Akaroa	8	en	1.03	4.57	2.94
Akaroa	8	en	1.25	5.39	3.61
Akaroa	8	en	1.07	5.43	3.01
Akaroa	8	en	1.35	5.03	2.76
Akaroa	9	eo	1.62	7.53	3.52
Akaroa	9	eo	1.46	7.43	3.33
Akaroa	9	eo	1.34	5.89	2.91
Akaroa	9	eo	1.46	6.33	2.76
Akaroa	9	eo	1.44	6.81	3.09
Akaroa	10	ep	1.28	7.88	2.64
Akaroa	10	ep	1.23	7.14	2.57
Akaroa	10	ep	1.37	7.73	3.07
Akaroa	10	ep	1.3	8.25	2.96
Akaroa	10	ep	1.26	6.87	3.09
Akaroa	11	eq	1.67	4.98	2.61
Akaroa	11	eq	1.33	4.53	2.24
Akaroa	11	eq	0.97	5.29	2.48
Akaroa	11	eq	1.34	4.98	2.7
Akaroa	11	eq	1.33	5.02	2.63
Akaroa	12	er	1.45	6.19	3.05
Akaroa	12	er	1.45	6.21	3.38
Akaroa	12	er	1.47	7.85	3.9
Akaroa	12	er	1.35	6.58	3.53
Akaroa	12	er	1.3	6.57	3.05
Akaroa	13	es	1.22	5.03	3.33
Akaroa	13	es	1.28	4.79	2.83
Akaroa	13	es	1.4	5.1	2.65
Akaroa	13	es	1.15	6.09	3.12
Akaroa	13	es	1.42	5.41	2.71
Akaroa	14	et	1.74	6.47	2.8
Akaroa	14	et	1.66	7.07	3.3
Akaroa	14	et	1.33	6.83	2.96
Akaroa	14	et	1.77	7.09	3.45
Akaroa	14	et	1.44	7.36	3.03
Akaroa	15	eu	1.77	5.83	2.88
Akaroa	15	eu	1.05	5.98	2.83
Akaroa	15	eu	1.81	5.34	2.84
Akaroa	15	eu	1.29	4.6	2.59
Akaroa	15	eu	1.56	5.83	2.89
Akaroa	16	ev	1.17	6.37	2.97
Akaroa	16	ev	1.81	5.76	2.66
Akaroa	16	ev	1.69	5.54	2.87

Akaroa	16	ev	1.24	6.27	2.99
Akaroa	16	ev	1.41	6.23	2.59
Akaroa	17	ew	1.27	6.05	2.96
Akaroa	17	ew	1.09	5.76	3.23
Akaroa	17	ew	1.25	5.76	2.6
Akaroa	17	ew	1.21	5.87	2.93
Akaroa	17	ew	1.16	6.08	2.82
Akaroa	18	ex	1.6	6.43	2.93
Akaroa	18	ex	2.02	5.94	3.07
Akaroa	18	ex	1.84	6.63	3.2
Akaroa	18	ex	1.81	6.54	2.78
Akaroa	18	ex	1.66	6.19	3.37
Akaroa	19	ey	1.78	5.19	2.4
Akaroa	19	ey	1.62	5.49	2.36
Akaroa	19	ey	1.41	7	2.52
Akaroa	19	ey	1.94	7.62	2.69
Akaroa	19	ey	1.42	7.63	2.74
Akaroa	20	ez	1.17	8.55	3.45
Akaroa	20	ez	1.26	7.84	2.87
Akaroa	20	ez	1.51	5.84	2.34
Akaroa	20	ez	1.11	8.65	3.09
Akaroa	20	ez	1.14	8.77	3.24
Akaroa	21	fa	1.7	8.41	2.97
Akaroa	21	fa	1.39	8.04	3.01
Akaroa	21	fa	1.33	6.55	2.54
Akaroa	21	fa	1.43	7.96	3.2
Akaroa	21	fa	1.71	8.06	2.8
Akaroa	22	fb	1.77	8.46	3.31
Akaroa	22	fb	1.45	6.89	3.13
Akaroa	22	fb	1.55	7.53	3.09
Akaroa	22	fb	1.57	6.81	2.73
Akaroa	22	fb	1.92	7.25	2.57
Akaroa	23	fc	1.56	6.83	2.86
Akaroa	23	fc	1.66	7.12	3.13
Akaroa	23	fc	1.61	7.53	3.2
Akaroa	23	fc	1.72	7.08	2.97
Akaroa	23	fc	1.51	6.1	2.76
Lake Forsyth	1	fd	1.13	5.95	2.61
Lake Forsyth	1	fd	0.98	5.53	2.43
Lake Forsyth	1	fd	1	5.12	2.49
Lake Forsyth	1	fd	1	5.89	3.04
Lake Forsyth	1	fd	1.36	5.79	2.92
Lake Forsyth	2	fe	1.17	4.54	2.45
Lake Forsyth	2	fe	1.28	4.78	2.81
Lake Forsyth	2	fe	1.17	4.99	2.94
Lake Forsyth	2	fe	1.32	4.24	2.66
Lake Forsyth	2	fe	1.29	4.99	2.82
Lake Forsyth	3	fg	1.22	5.26	2.9
Lake Forsyth	3	fg	1.27	5.71	3.62

Lake Forsyth	3	fg	1.31	5.28	2.94
Lake Forsyth	3	fg	1.23	5.24	2.91
Lake Forsyth	3	fg	1.25	6	2.94
Lake Forsyth	4	fh	1.18	6.26	2.98
Lake Forsyth	4	fh	1.18	6.27	2.9
Lake Forsyth	4	fh	1.37	5.87	2.71
Lake Forsyth	4	fh	1.11	6.67	2.74
Lake Forsyth	4	fh	1.09	6.01	2.54
Lake Forsyth	5	fi	1.28	5.44	2.61
Lake Forsyth	5	fi	1.4	4.94	2.65
Lake Forsyth	5	fi	1.18	5.39	2.44
Lake Forsyth	5	fi	1.17	5.24	2.17
Lake Forsyth	5	fi	1.27	5.27	2.02
Lake Forsyth	6	fj	1.44	5.02	2.41
Lake Forsyth	6	fj	1.41	5.9	2.83
Lake Forsyth	6	fj	1.35	6.12	2.32
Lake Forsyth	6	fj	1.52	5.69	2.29
Lake Forsyth	6	fj	1.4	6.07	2.88
Lake Forsyth	7	fk	1.7	5.74	2.51
Lake Forsyth	7	fk	1.46	4.87	2.3
Lake Forsyth	7	fk	1.43	5.5	2.05
Lake Forsyth	7	fk	1.49	5.24	2.47
Lake Forsyth	7	fk	1.53	5.32	2.71
Lake Forsyth	8	fl	1.3	5.03	2.74
Lake Forsyth	8	fl	1.47	4.64	2.29
Lake Forsyth	8	fl	1.24	4.96	2.63
Lake Forsyth	8	fl	1.26	5.68	2.15
Lake Forsyth	8	fl	1.28	4.69	2.58
Lake Forsyth	9	fm	1.26	5.93	2.69
Lake Forsyth	9	fm	1.1	6.55	3.1
Lake Forsyth	9	fm	1.34	6.61	3.32
Lake Forsyth	9	fm	1.49	6.8	2.98
Lake Forsyth	9	fm	1.34	7.09	3.5
Lake Forsyth	10	fn	1.2	6.93	2.69
Lake Forsyth	10	fn	1.06	5.87	3.1
Lake Forsyth	10	fn	1.11	6.55	2.91
Lake Forsyth	10	fn	1.15	5.87	2.87
Lake Forsyth	10	fn	1.36	5.87	2.81
Lake Forsyth	11	fo	1.35	5.2	2.5
Lake Forsyth	11	fo	1.54	5.42	2.25
Lake Forsyth	11	fo	1.27	5.87	2.43
Lake Forsyth	11	fo	1.76	6.19	2.37
Lake Forsyth	11	fo	1.45	5.74	2.84
Lake Forsyth	12	fp	1.24	6.79	2.89
Lake Forsyth	12	fp	1.6	6.9	3.13
Lake Forsyth	12	fp	1.5	5.7	2.33
Lake Forsyth	12	fp	1.37	7.06	2.81
Lake Forsyth	12	fp	1.71	7.59	2.9
Lake Forsyth	13	fq	1.51	4.87	2.41

Lake Forsyth	13	fq	1.19	4.27	1.9
Lake Forsyth	13	fq	1.53	5.06	2.39
Lake Forsyth	13	fq	1.67	4.72	2.43
Lake Forsyth	13	fq	1.72	5.11	2.34
Lake Forsyth	14	fr	1.41	5.28	2.82
Lake Forsyth	14	fr	1.28	5.58	1.91
Lake Forsyth	14	fr	1.49	5.74	2.13
Lake Forsyth	14	fr	1.44	5.87	2.28
Lake Forsyth	14	fr	1.24	5.86	2.46
Lake Forsyth	15	fs	1.39	6.03	2.57
Lake Forsyth	15	fs	1.04	4.93	2.15
Lake Forsyth	15	fs	1.4	5.82	2.66
Lake Forsyth	15	fs	1.17	6.77	2.48
Lake Forsyth	15	fs	1.18	5.93	2.63
Lake Forsyth	16	ft	0.99	4.82	2.64
Lake Forsyth	16	ft	1.14	4.82	2.27
Lake Forsyth	16	ft	1.08	5.07	2.6
Lake Forsyth	16	ft	1.16	4.18	2.11
Lake Forsyth	16	ft	1.49	4.64	2.36
Lake Forsyth	17	fu	1.18	4.8	2.71
Lake Forsyth	17	fu	1.2	5.26	2.76
Lake Forsyth	17	fu	1.36	5.71	2.49
Lake Forsyth	17	fu	1.39	4.4	3.04
Lake Forsyth	17	fu	1.19	5.6	2.25
Lake Forsyth	18	fv	1.13	4.03	2.31
Lake Forsyth	18	fv	1.03	4.07	2.22
Lake Forsyth	18	fv	1.36	4.39	2.12
Lake Forsyth	18	fv	1.35	4.78	2.01
Lake Forsyth	18	fv	1.07	4.45	2.2
Lake Forsyth	19	fw	1.47	6.17	2.87
Lake Forsyth	19	fw	1.21	5.79	3.07
Lake Forsyth	19	fw	1.39	5.3	2.79
Lake Forsyth	19	fw	1.93	5.66	2.92
Lake Forsyth	19	fw	1.27	5.73	2.93
Lake Forsyth	20	fx	1.58	5.93	2.83
Lake Forsyth	20	fx	1.29	5.46	2.39
Lake Forsyth	20	fx	1.53	6.07	2.61
Lake Forsyth	20	fx	1.52	6.57	2.74
Lake Forsyth	20	fx	1.47	5.69	2.27
Lake Forsyth	21	fy	1.02	4.85	2.88
Lake Forsyth	21	fy	1.3	5.84	2.92
Lake Forsyth	21	fy	1.38	4.66	3.02
Lake Forsyth	21	fy	1.53	5.84	2.82
Lake Forsyth	21	fy	1.5	5.55	2.9
Lake Forsyth	22	fz	1.35	4	2.32
Lake Forsyth	22	fz	1.05	4.79	2.59
Lake Forsyth	22	fz	1.01	4.48	2.68
Lake Forsyth	22	fz	1.18	4.91	2.27
Lake Forsyth	22	fz	1.03	4.39	2.32

Lake Forsyth	23	ga	1.34	5.28	2.39
Lake Forsyth	23	ga	1.7	5.14	2.6
Lake Forsyth	23	ga	1.3	4.82	2.04
Lake Forsyth	23	ga	1.46	5.09	2.31
Lake Forsyth	23	ga	1.4	5.3	2.35
Lake Forsyth	24	gb	1.32	6.25	2.35
Lake Forsyth	24	gb	1.74	7.29	2.61
Lake Forsyth	24	gb	1.32	5.81	2.38
Lake Forsyth	24	gb	1.32	5.89	2.56
Lake Forsyth	24	gb	1.29	6.94	2.63
Lake Forsyth	25	gc	1.44	6.06	2.97
Lake Forsyth	25	gc	1.95	5.85	2.5
Lake Forsyth	25	gc	1.46	5.31	2.38
Lake Forsyth	25	gc	1.67	5.23	2.47
Lake Forsyth	25	gc	1.98	6.23	2.5
Lake Forsyth	26	gd	1.34	6.69	2.88
Lake Forsyth	26	gd	1.38	7.25	2.92
Lake Forsyth	26	gd	1.16	7.48	2.7
Lake Forsyth	26	gd	1.08	7.73	3
Lake Forsyth	26	gd	1.41	9.21	2.79
Lake Forsyth	27	ge	1.1	4.02	2.2
Lake Forsyth	27	ge	1.05	4	2.16
Lake Forsyth	27	ge	1.2	4.74	2.27
Lake Forsyth	27	ge	1.32	4.73	2.24
Lake Forsyth	27	ge	1.26	4.42	2.69
Lake Forsyth	28	gf	1.36	7.18	3.04
Lake Forsyth	28	gf	1.36	6.8	3.1
Lake Forsyth	28	gf	1.07	6.81	2.94
Lake Forsyth	28	gf	1.55	6.14	2.93
Lake Forsyth	28	gf	1.47	6.15	3.06
Lake Forsyth	29	gg	1.04	4.97	2.25
Lake Forsyth	29	gg	1.05	5.39	2.3
Lake Forsyth	29	gg	1.15	4.86	2.33
Lake Forsyth	29	gg	0.98	5.27	2.38
Lake Forsyth	29	gg	1.42	5.17	2.22
Lake Forsyth	30	gh	1.63	5.01	2.31
Lake Forsyth	30	gh	1.34	5.31	2.58
Lake Forsyth	30	gh	1.54	6.21	2.39
Lake Forsyth	30	gh	1.27	6.23	2.88
Lake Forsyth	30	gh	1.49	5.65	2.59
Mt Cavendish	1	gi	2.26	7	2.88
Mt Cavendish	1	gi	1.92	6.6	2.36
Mt Cavendish	1	gi	1.78	6.61	2.77
Mt Cavendish	1	gi	1.76	5.88	2.36
Mt Cavendish	1	gi	1.75	5.63	2.59
Mt Cavendish	2	gj	1.77	6.68	3.32
Mt Cavendish	2	gj	1.9	7.14	3.7
Mt Cavendish	2	gj	1.72	7.18	3.5
Mt Cavendish	2	gj	1.99	6.67	3.27

Mt Cavendish	2	gj	1.8	7.55	3.9
Mt Cavendish	3	gk	1.41	5.39	2.39
Mt Cavendish	3	gk	1.35	6.05	2.84
Mt Cavendish	3	gk	1.31	5.57	3.08
Mt Cavendish	3	gk	1.29	5.69	2.99
Mt Cavendish	3	gk	1.55	4.58	1.84
Mt Cavendish	4	gl	1.92	6.65	3.67
Mt Cavendish	4	gl	1.66	5.84	3.07
Mt Cavendish	4	gl	1.98	6.32	2.91
Mt Cavendish	4	gl	1.75	5.48	3.16
Mt Cavendish	4	gl	1.54	5.99	3.03
Mt Cavendish	5	gm	2.08	8.23	2.87
Mt Cavendish	5	gm	1.76	6.78	2.81
Mt Cavendish	5	gm	1.71		
Mt Cavendish	5	gm	1.98		
Mt Cavendish	5	gm	1.81		
Mt Cavendish	6	gn	1.46	6.83	2.87
Mt Cavendish	6	gn	1.53	6.02	2.6
Mt Cavendish	6	gn	1.62	6.56	2.6
Mt Cavendish	6	gn	1.8	6.73	2.83
Mt Cavendish	6	gn	1.53	6.44	2.44
Mt Cavendish	7	go	1.71	6.66	2.77
Mt Cavendish	7	go	1.41	5.75	2.06
Mt Cavendish	7	go	1.83	5.43	1.67
Mt Cavendish	7	go	1.17	7.48	3.05
Mt Cavendish	7	go	1.32	6.85	2.66
Mt Cavendish	8	gp	2.37	4.39	1.86
Mt Cavendish	8	gp	2.02	5.46	2.9
Mt Cavendish	8	gp	2.06	5.55	2.24
Mt Cavendish	8	gp	1.73	4.92	1.97
Mt Cavendish	8	gp	2.22	5.52	2.03
Mt Cavendish	9	gq	1.91	6.44	2.8
Mt Cavendish	9	gq	2.05	5.75	2.66
Mt Cavendish	9	gq	1.71	5.08	2.36
Mt Cavendish	9	gq	1.69	6.05	2.69
Mt Cavendish	9	gq	1.6	7.2	2.65
Mt Cavendish	10	gr	2.22	7.95	2.86
Mt Cavendish	10	gr	1.83	7.27	2.88
Mt Cavendish	10	gr	2.01	8.79	3.18
Mt Cavendish	10	gr	1.74	7.02	2.15
Mt Cavendish	10	gr	1.89	8.3	2.73
Mt Cavendish	11	gs	1.62	7.06	2.76
Mt Cavendish	11	gs	2.25	7.5	3.1
Mt Cavendish	11	gs	1.87	8.35	3.41
Mt Cavendish	11	gs	2.01		
Mt Cavendish	11	gs	1.95		
Mt Cavendish	12	gt	1.9	8.29	3.19
Mt Cavendish	12	gt	1.88	7.76	3.25
Mt Cavendish	12	gt	2.05	8.43	3.05

Mt Cavendish	12	gt	1.85	7.25	2.82
Mt Cavendish	12	gt	1.65	9.19	2.6
Mt Cavendish	13	gu	1.73	6.21	2.84
Mt Cavendish	13	gu	1.58	5.86	2.59
Mt Cavendish	13	gu	1.61	6.74	2.47
Mt Cavendish	13	gu	1.75	5.74	2.44
Mt Cavendish	13	gu	1.45	6.49	2.63
Mt Cavendish	14	gv	2.24	7.42	2.84
Mt Cavendish	14	gv	2.13	7.36	3.25
Mt Cavendish	14	gv	2.06	7.59	2.76
Mt Cavendish	14	gv	1.96	8.2	3.23
Mt Cavendish	14	gv	2	7.56	3.26
Mt Cavendish	15	gw	2.35	8.1	2.82
Mt Cavendish	15	gw	1.83	8.17	2.97
Mt Cavendish	15	gw	2.06	8.99	2.72
Mt Cavendish	15	gw	2	9.72	3
Mt Cavendish	15	gw	2.14	9.86	2.9
Mt Cavendish	16	gx	1.84	7.44	3.46
Mt Cavendish	16	gx	2.11	6.83	3.36
Mt Cavendish	16	gx	1.83	6.25	3.13
Mt Cavendish	16	gx	1.94	7.21	3.43
Mt Cavendish	16	gx	1.74	7.21	3.62
Mt Cavendish	17	gy	1.63	6.81	2.91
Mt Cavendish	17	gy	1.42	5.95	2.5
Mt Cavendish	17	gy	1.88	6.71	2.87
Mt Cavendish	17	gy	1.63	7.2	3.21
Mt Cavendish	17	gy	1.61	5.57	2.42
Mt Cavendish	18	gz	1.43	6.71	2.82
Mt Cavendish	18	gz	1.52	6.91	2.73
Mt Cavendish	18	gz	1.65		
Mt Cavendish	18	gz	1.79		
Mt Cavendish	18	gz	1.47		
Mt Cavendish	19	ha	2.01	7.56	3.72
Mt Cavendish	19	ha	1.85	7.45	3.21
Mt Cavendish	19	ha	1.87	6.93	3.68
Mt Cavendish	19	ha	2	7.25	3.24
Mt Cavendish	19	ha	1.86	6.36	2.99
Mt Cavendish	20	hb	2.13	9.39	3.19
Mt Cavendish	20	hb	1.96	9.44	2.97
Mt Cavendish	20	hb	1.95	9.76	3.23
Mt Cavendish	20	hb	2.18	8.07	2.95
Mt Cavendish	20	hb	1.72	9.66	3.17
Mt Cavendish	21	hc	2.39	6.82	3.43
Mt Cavendish	21	hc	2.27	7.04	3.47
Mt Cavendish	21	hc	1.8	6.83	3.12
Mt Cavendish	21	hc	2.29	5.66	2.26
Mt Cavendish	21	hc	2.3		
Mt Cavendish	22	hd	2.11	6.47	3.3
Mt Cavendish	22	hd	1.62	6.58	3.04

Mt Cavendish	22	hd	1.69	5.75	3.02
Mt Cavendish	22	hd	1.75	6.48	2.99
Mt Cavendish	22	hd	1.75	7.66	3.35
Ellesmere	1	he	1.45	5.27	2.38
Ellesmere	1	he	1.56	5.18	2.51
Ellesmere	1	he	1.23	5.18	2.31
Ellesmere	1	he	1.49	5.25	2.32
Ellesmere	1	he	1.46	5.23	2.05
Ellesmere	2	hf	1.12	8.25	3.97
Ellesmere	2	hf	1.38	7.61	3.3
Ellesmere	2	hf	1.42	7.07	3.23
Ellesmere	2	hf	1.27	6.53	2.8
Ellesmere	2	hf	1.2		
Ellesmere	3	hg	1.47	6.79	2.84
Ellesmere	3	hg	1.54	7.8	2.97
Ellesmere	3	hg	1.15	6.6	3.03
Ellesmere	3	hg	1.56	5.56	2.53
Ellesmere	3	hg	1.45	6.44	3.49
Ellesmere	4	hi	1.43	6.19	3.1
Ellesmere	4	hi	1.22	5.48	2.87
Ellesmere	4	hi	1.21	6.26	2.69
Ellesmere	4	hi	1.1	6.33	2.7
Ellesmere	4	hi	1.2	5.98	2.69
Ellesmere	5	hj	1.31	7.21	2.98
Ellesmere	5	hj	1.41	7.65	3.05
Ellesmere	5	hj	1.31	7.17	2.83
Ellesmere	5	hj	1.12	7.76	2.89
Ellesmere	5	hj	1.34	8.48	3.08
Ellesmere	6	hk	1.45	6.93	2.98
Ellesmere	6	hk	1.49	7.76	3.33
Ellesmere	6	hk	1.57	7.05	3.43
Ellesmere	6	hk	1.64	5.59	2.96
Ellesmere	6	hk	1.28	6.62	2.49
Ellesmere	7	hl	1.39	8.37	3.25
Ellesmere	7	hl	1.47	8.5	3.58
Ellesmere	7	hl	1.74	8.03	3.14
Ellesmere	7	hl	1.35	8	3.03
Ellesmere	7	hl	1.49	8.49	3.4
Ellesmere	8	hm	1.49	6.82	3.23
Ellesmere	8	hm	1.32	6.96	3.33
Ellesmere	8	hm	1.4	8.37	3.12
Ellesmere	8	hm	1.34	7.56	2.81
Ellesmere	8	hm	1.6	6.89	2.72
Ellesmere	9	hn	1.76	5.73	2.32
Ellesmere	9	hn	1.74	6.43	2.47
Ellesmere	9	hn	1.28	6.29	2.25
Ellesmere	9	hn	1.47	6.95	2.91
Ellesmere	9	hn	1.52	7	2.32
Ellesmere	10	ho	1.71	7.54	2.81

Ellesmere	10	ho	1.8	7.01	2.77
Ellesmere	10	ho	1.84	7.97	2.92
Ellesmere	10	ho	1.79	6.69	2.73
Ellesmere	10	ho	1.75	7.73	3.32
Ellesmere	11	hp	1.91	7.86	3.19
Ellesmere	11	hp	1.79	7.87	3.38
Ellesmere	11	hp	1.79	8.43	3.32
Ellesmere	11	hp	1.8	8.43	2.99
Ellesmere	11	hp	1.53	8.86	3.21
Ellesmere	12	hq	1.55	5.82	2.43
Ellesmere	12	hq	1.47	5.29	2.4
Ellesmere	12	hq	1.52	5.3	2.7
Ellesmere	12	hq	1.36	6.44	2.62
Ellesmere	12	hq	1.63	6.63	2.7
Ellesmere	13	hr	1.52	7.14	2.96
Ellesmere	13	hr	1.61	7.78	3.15
Ellesmere	13	hr	1.32	8.46	3.36
Ellesmere	13	hr	1.52	8.17	3.2
Ellesmere	13	hr	1.5	7.17	3.17
Ellesmere	14	hs	1.41	6.74	3.02
Ellesmere	14	hs	1.26	6.71	2.83
Ellesmere	14	hs	1.63	7.49	2.81
Ellesmere	14	hs	1.39	6.17	2.53
Ellesmere	14	hs	1.26	6.67	2.71
Ellesmere	15	ht	2.03	5.89	2.88
Ellesmere	15	ht	2.07	5.9	2.87
Ellesmere	15	ht	1.96	7.44	3.05
Ellesmere	15	ht	1.48	4.33	2.02
Ellesmere	15	ht	1.53	5.43	2.78
Ellesmere	16	hu	1.97	8.18	2.82
Ellesmere	16	hu	2	6.44	2.56
Ellesmere	16	hu	1.8	7.04	2.6
Ellesmere	16	hu	1.96	6.25	2.78
Ellesmere	16	hu	1.3	7.01	3.06
Ellesmere	17	hv	2.28	6.18	2.88
Ellesmere	17	hv	2.05	6.34	2.9
Ellesmere	17	hv	2.09	6.68	3.14
Ellesmere	17	hv	2.1	5.93	3.06
Ellesmere	17	hv	2.35	5.52	2.75
Ellesmere	18	hw	1.83	5.37	2.42
Ellesmere	18	hw	1.63	6.04	2.7
Ellesmere	18	hw	1.8	5.71	2.75
Ellesmere	18	hw	1.87	6.07	2.73
Ellesmere	18	hw	1.57	5.25	2.56
Ellesmere	19	hx	2.06	6.6	2.5
Ellesmere	19	hx	2.32	6.83	2.79
Ellesmere	19	hx	1.6	7.17	3
Ellesmere	19	hx	1.79	6.57	2.75
Ellesmere	19	hx	2.25		

Ellesmere	20	hy	1.94	5.54	2.97
Ellesmere	20	hy	1.62	5.56	2.83
Ellesmere	20	hy	1.61	4.99	2.48
Ellesmere	20	hy	1.97	5.58	2.85
Ellesmere	20	hy	1.83	5.63	2.65
Ellesmere	21	hz	1.81	6.17	2.53
Ellesmere	21	hz	1.67	6.86	2.84
Ellesmere	21	hz	1.51	7.74	3.04
Ellesmere	21	hz	1.4	7.32	3.04
Ellesmere	21	hz	1.72	7.07	2.95
Ellesmere	22	ia	1.61	6.68	2.92
Ellesmere	22	ia	1.6	6.19	2.41
Ellesmere	22	ia	1.37	6.2	3.42
Ellesmere	22	ia	2.03	6.37	2.95
Ellesmere	22	ia	1.48	6.51	2.97
Ellesmere	23	ib	1.51	6.3	3.12
Ellesmere	23	ib	1.54	6.42	3.25
Ellesmere	23	ib	1.28	7.49	3.23
Ellesmere	23	ib	1.25	7.13	3.21
Ellesmere	23	ib	1.55	7.1	3.49
Ellesmere	24	ic	1.43	5.83	2.71
Ellesmere	24	ic	1.53	5.88	2.81
Ellesmere	24	ic	1.46	5.48	2.79
Ellesmere	24	ic	1.66	6.29	2.94
Ellesmere	24	ic	2.02	5.39	2.95
Ellesmere	25	id	2.03	7.38	2.99
Ellesmere	25	id	1.9	7.27	3.02
Ellesmere	25	id	1.53	7.68	2.67
Ellesmere	25	id	1.75	6.91	2.75
Ellesmere	25	id	1.88	7.01	3.09
Taumarunui	1	ie	1.38	5.96	4.18
Taumarunui	1	ie	1.44	5.4	4.07
Taumarunui	1	ie	1.51	6.07	4.56
Taumarunui	1	ie	1.13	5.69	4.57
Taumarunui	1	ie	1.28	4.54	3.49
Taumarunui	2	if	1.21	7.1	4.53
Taumarunui	2	if	1.84	7.81	4.63
Taumarunui	2	if	1.2	6.9	4.33
Taumarunui	2	if	1.47	7.83	4.79
Taumarunui	2	if	1.29	8	4.27
Taumarunui	3	ig	1.26	5.9	3.33
Taumarunui	3	ig	1.35	4.73	3.3
Taumarunui	3	ig	1.54	5.52	3.1
Taumarunui	3	ig	1.57	6.71	3.39
Taumarunui	3	ig	1.26	5.61	3.01
Taumarunui	4	ih	1.44	7.68	5.19
Taumarunui	4	ih	1.2	9.56	5.24
Taumarunui	4	ih	1.26	7.41	4.13
Taumarunui	4	ih	1.4	7.78	4.96

Taumarunui	4	ih	1.67	8.29	4.56
Taumarunui	5	ij	1.27	5.15	3.41
Taumarunui	5	ij	1.48	5.73	3.46
Taumarunui	5	ij	1.27	5.35	3.88
Taumarunui	5	ij	1.7	5.43	3.45
Taumarunui	5	ij	1.25	5.31	3.29
Taumarunui	6	ik	1.47	6.5	3.95
Taumarunui	6	ik	1.41	6.12	3.85
Taumarunui	6	ik	1.78	6.89	3.92
Taumarunui	6	ik	1.45	5.65	3.68
Taumarunui	6	ik	1.46	5.76	3.21
Taumarunui	7	il	1.13	6.78	4
Taumarunui	7	il	1.23	6.5	4.87
Taumarunui	7	il	1.12	5.79	4.01
Taumarunui	7	il	1.24	6.32	4.52
Taumarunui	7	il	1.1	5.79	4.09
Taumarunui	8	im	1.2	7.56	4.43
Taumarunui	8	im	1.14	5.78	4.04
Taumarunui	8	im	1.16	7.3	4.9
Taumarunui	8	im	1.53	7.39	4.58
Taumarunui	8	im	1.37	6.04	3.52
Manawatu	1	in	1.27	5.45	2.94
Manawatu	1	in	1.13	5.94	3.02
Manawatu	1	in	1.27	5.62	3.2
Manawatu	1	in	1.53	7.42	4.46
Manawatu	1	in	1.48	5.65	3.38
Manawatu	2	io	1.26	5.33	3.87
Manawatu	2	io	1.22	5.34	3.33
Manawatu	2	io	1.37	5.46	3.97
Manawatu	2	io	1.22	5.73	3.47
Manawatu	2	io	1.13	6.06	4.33
Manawatu	3	ip	1.28	4.16	3.28
Manawatu	3	ip	1.01	4.13	3.32
Manawatu	3	ip	1.21	4.32	3.19
Manawatu	3	ip	1.1	4.07	3.18
Manawatu	3	ip	1.4	4.54	3.45
Manawatu	4	iq	1.28	6.53	3.37
Manawatu	4	iq	1.19	5.21	3.7
Manawatu	4	iq	1.41	5.93	3.18
Manawatu	4	iq	1.26	7.69	3.88
Manawatu	4	iq	1.13	6.65	3.33
Manawatu	5	ir	1.55	7.25	3.81
Manawatu	5	ir	1.35	9.26	4.17
Manawatu	5	ir	1.38	8.54	3.48
Manawatu	5	ir	1.48	9.29	3.51
Manawatu	5	ir	1.37	9.77	3.9
Manawatu	6	is	1.54	6.38	4.07
Manawatu	6	is	1.57	5.68	3.94
Manawatu	6	is	2.17	6.85	4.32

Manawatu	6	is	1.94	6.41	3.64
Manawatu	6	is	1.63	6.15	4.08
Manawatu	7	it	1.28	6.34	3.61
Manawatu	7	it	1.48	4.69	3.02
Manawatu	7	it	1.37	5.34	3.3
Manawatu	7	it	1.41	5.46	3.72
Manawatu	7	it	1.34	6.13	3.38
Tongariro	1	iu	1.57	6.4	3.44
Tongariro	1	iu	1.79	5.8	3.07
Tongariro	1	iu	2.1	6.38	3.54
Tongariro	1	iu	1.57	5.62	3.09
Tongariro	1	iu	1.74	6.06	3.06
Tongariro	2	iv	2.01	6.65	2.86
Tongariro	2	iv	2.07	6.66	2.98
Tongariro	2	iv	2.02	6.24	3.08
Tongariro	2	iv	2.18	7.53	3.04
Tongariro	2	iv	1.93	6.9	3.18
Tongariro	3	iw	2.03	7.94	3.52
Tongariro	3	iw	2.35	7.17	3.27
Tongariro	3	iw	1.9	7.5	3.18
Tongariro	3	iw	2.22	7.42	3.34
Tongariro	3	iw	2.24	6.95	3.11
Tongariro	4	ix	1.81	6.81	3.38
Tongariro	4	ix	1.6	7.44	3.27
Tongariro	4	ix	2.01	7.7	3.13
Tongariro	4	ix	1.74	6.16	2.99
Tongariro	4	ix	1.89	7.44	3.49
Tongariro	5	iy	2.79	7.3	3.41
Tongariro	5	iy	2.74	7.45	3.13
Tongariro	5	iy	2.67	8.18	3.7
Tongariro	5	iy	2.78	8.07	3.25
Tongariro	5	iy	2.18	8.01	3.29
Tongariro	6	iz	2.14	5.38	3.12
Tongariro	6	iz	1.95	4.52	2.88
Tongariro	6	iz	2.09	5.28	3.07
Tongariro	6	iz	2.19	5.43	2.97
Tongariro	6	iz	2.25	6.08	3.27
Tongariro	7	ja	2.41	8.21	3.83
Tongariro	7	ja	2.56	7.55	3.84
Tongariro	7	ja	2.37	7.58	3.59
Tongariro	7	ja	2.53	8.13	3.61
Tongariro	7	ja	2.13	8.89	3.77
Tongariro	8	jb	1.84	7.43	3.35
Tongariro	8	jb	1.96	7.92	3.06
Tongariro	8	jb	2	7.31	3.22
Tongariro	8	jb	1.77	6.91	2.87
Tongariro	8	jb	2.12	7.3	3.11
Tongariro	9	jc	2.1	5.38	3.25
Tongariro	9	jc	2.34	5.4	3.15

Tongariro	9	jc	1.92	5.58	3.06
Tongariro	9	jc	1.91	5.56	3.09
Tongariro	9	jc	2.22	5.68	3.2
Tongariro	10	jd	2.13	5.97	2.99
Tongariro	10	jd	2.13	6.65	2.83
Tongariro	10	jd	1.77	6.87	3.5
Tongariro	10	jd	2.48	6.8	2.98
Tongariro	10	jd	2.43	7.24	2.86
Tongariro	11	je	2.88	7.33	3.2
Tongariro	11	je	2.26	8.2	3.55
Tongariro	11	je	2.7	10.05	3.34
Tongariro	11	je	2.31	8.53	3.41
Tongariro	11	je	2.42	7.27	3.17
Tongariro	12	jf	2.3	5.67	3.54
Tongariro	12	jf	2.15	5.93	3.7
Tongariro	12	jf	2.51	5.64	3.6
Tongariro	12	jf	2.09	6.64	3.94
Tongariro	12	jf	2.12	6.35	3.9
Tongariro	13	jg	2.15	4.39	3.07
Tongariro	13	jg	2.06	5.46	3.75
Tongariro	13	jg	2.27	6.64	4.02
Tongariro	13	jg	1.71	4.98	3.52
Tongariro	13	jg	2.2	6.4	3.52
Tongariro	14	jh	1.67	7.41	3.99
Tongariro	14	jh	1.88	6.48	3.53
Tongariro	14	jh	2.14	6.42	3.55
Tongariro	14	jh	2.25	6.35	3.44
Tongariro	14	jh	2.01	6.57	3.71
Tongariro	15	ji	2.29	8.43	4.11
Tongariro	15	ji	2.09	8.77	3.89
Tongariro	15	ji	1.82	8.6	4.07
Tongariro	15	ji	1.93	9.48	4.13
Tongariro	15	ji	2.11	9.39	4.11
Tongariro	16	jk	2.23	7.42	4.14
Tongariro	16	jk	1.96	6.39	3.01
Tongariro	16	jk	1.94	7.52	4.11
Tongariro	16	jk	1.93	5.89	3.99
Tongariro	16	jk	2.02	7.41	3.69
Mt Egmont	1	jk	2.57	9.87	4.78
Mt Egmont	1	jk	2.09	8.25	4.37
Mt Egmont	1	jk	2.69	9.83	5.02
Mt Egmont	1	jk	2.34	8.83	5.01
Mt Egmont	1	jk	2.18	8.48	4.52
Mt Egmont	2	jm	2.41	8.33	4.22
Mt Egmont	2	jm	2.12	9.33	4.2
Mt Egmont	2	jm	2.09	8.93	4.12
Mt Egmont	2	jm	2.28	9.35	4.47
Mt Egmont	2	jm	2	9.33	4.25
Mt Egmont	3	jn	3.28	8.34	4.82

Mt Egmont	3	jn	2.04	9.22	5.41
Mt Egmont	3	jn	3.07	8.04	5.33
Mt Egmont	3	jn	2.5	9.03	5.42
Mt Egmont	3	jn	2.72	7.94	4.37

Appendix 2 Collection data for shrubs and trees examined for wood anatomy (Chapter 4). All are from the South Island.

	Plants		Wood disc					
Species	No.	Height	Diameter (cm)	Approx. no. of growth rings	Locality	Soil type	Mean annual rainfall*	CHR voucher
Ca. australis	1	1.5 m	2.0	9	Kaitorete Spit, Canterbury	Shallow soil	666	496553
	2	1.2 m	3.0	16	McKenzie Pass, Canterbury	Shallow soil	731	497354
Ca. compacta	1	1 m	2.0	26	Kawarau River, Otago	Shallow, stony soil	401	496515
	2	1 m	2.0	9	Cultivated at Lincoln, Canterbury	Deep soil	666	496560
Ca. corrugata	1	5 cm	0.5	11	Kaitorete Spit, Canterbury	Coastal gravels	666	496554
	2	5 cm	0.5	12	Kaitorete Spit, Canterbury	Coastal gravels	666	496555
	3	5 cm	0.5	6	McKenzie Pass, Canterbury	Stony, gravelly soil	731	497358
Ca. monroi	1	15 cm	1.5	19	McKenzie Pass, Canterbury	Shallow, stony soil	731	497355
	2	10 cm	1.3	13	McKenzie Pass, Canterbury	Shallow, stony soil	731	497356
Ca. nana	1	10 cm	2.0	22	Dry Stream, Canterbury	Alluvial gravels	-	496572

Appendix 2 continued

Species	No.	Height	Diameter	Growth rings	Locality	Soil type	Rainfall	CHR
	2	10 cm	2.0	16	Lake Aviemore, Otago	Stony, shingly soil	528	496577
	3	10 cm	2.2	11	McKenzie Pass, Canterbury	Stony, shingly soil	731	497353
	4	10 cm	1.5	16	Lake Waitaki, Canterbury	Alluvial gravels	528	497357
Ca. odorata	1	2 m	3.8	15	Cultivated at Lincoln, Canterbury	Deep soil	666	497359
	2	2 m	4.0	14	Cultivated at Dunedin, Otago	Deep soil	938	496605
Ca. petriei	1	2 m	4.0	22	Omarama, Otago	Stony soil	528	496574
	2	1.5 m	3.0	23	Lake Aviemore, Otago	Stony soil	528	496576
	3	2.2 m	4.0	20	Lake Pukaki, Canterbury	Shallow, stony soil	641	496575
Ca. williamsii	1	1.2 m	2.5	10	Cultivated at Dunedin, Otago	Deep soil	938	496563
	2	5 m	3.8	15	Cultivated at Christchurch, Canterbury	Deep soil	666	496606
Ch. muritai	1	2.5 m	6.5	14	Cultivated at Lincoln, Canterbury	Deep soil	666	496561

Appendix 2 continued

Species	No.	Height	Diameter	Grwoth rings	Locality	Soil type	Rainfall	CHR
	2	2.5 m	7.0	15	Cultivated at Lincoln, Canterbury	Deep soil	666	496607
	3	4 m	5.0	23	Clifford Bay, Marlborough	Alluvial gravels	591	496608
Ch. stevensonii	1	2.5 m	5.3	16	Cultivated at Lincoln, Canterbury	Deep soil	666	497371
	2	2.5 m	6.5	17	Cultivated at Lincoln, Canterbury	Deep soil	666	497372
Co. crassicaule	1	0.5 m	1.9	22	Porters Pass, Canterbury	Yellow-brown soil	801	496569
	2	2 m	2.6	27	Lake Tekapo, Canterbury	Stony soil	597	496578
	3	2 m	2.6	22	Lake Ohau, Canterbury	Stony soil	646	496579
N. carmichaeliae	1	3.5 m	6.5	32	Spray River, Marlborough	Shallow, stony soil	876	496609
	2	4 m	7.3	35	Spray River, Marlborough	Shallow, stony soil	876	496610
	3	2.5 m	6.0	18	Spray Point, Marlborough	Shallow soil	876	496611
N. glabrescens	1	2.5 m	6.0	16	Clarence River, Marlborough	Alluvial gravels	888	496614

Appendix 2 continued

Species	No.	Height	Diameter	Growth rings	Locality	Soil type	Rainfall	CHR
	2	2.2 m	4.5	10	Cultivated at Lincoln, Canterbury	Deep soil	666	497370
	3	2.2 m	4.7	12	Cultivated at Lincoln, Canterbury	Deep soil	666	497369
N. torulosum	1	2 m	5.0	14	Cultivated at Lincoln, Canterbury	Deep soil	666	496562
	2	3 m	5.5	33	Lynn Stream, Canterbury	Yellow-brown soil	944	496612
	3	4 m	8.5	38	Lynn Stream, Canterbury	Yellow-brown soil	944	496613

* Taken from New Zealand Meterological Service Miscellaneous Publication 177. Summaries of Climatological Observations to 1980. Mean annual rainfall for a particular site is taken from the nearest climatological station. For example, the Peel Forest Station is closest to Lynn Stream.

Appendix 3 Raw data for the statistical analysis of wood anatomy characters for *Carmichaelia* (*Ca.*), *Chordospartium* (*Ch.*), *Corallosprtium* (*Co.*), and *Notospartium* (*N.*). A = vessel diameter; B = vessel length; C = vessels per group; D = ray height; E = ray width; F = fibre length.

Taxon	Accession	A	B	C	D	E	F
Ch. muritai	W2/4/1mur	30	0.145	9	0.64	4	1.04
Ch. muritai	W2/4/1mur	35	0.155	7	0.68	11	0.67
Ch. muritai	W2/4/1mur	25	0.145	6	0.67	11	0.83
Ch. muritai	W2/4/1mur	47	0.14	17	0.52	3	0.96
Ch. muritai	W2/4/1mur	45	0.1	21	0.85	10	0.83
Ch. muritai	W2/4/1mur	5	0.157	15	0.62	12	0.79
Ch. muritai	W2/4/1mur	35	0.115	9	0.83	5	1.04
Ch. muritai	W2/4/1mur	15	0.125	2	0.86	9	0.92
Ch. muritai	W2/4/1mur	22.5	0.15	12	0.86	8	0.93
Ch. muritai	W2/4/1mur	32.5	0.135	9	0.36		0.97
Ch. muritai	W2/4/1mur	17.5	0.125	13	0.31		0.69
Ch. muritai	W2/4/1mur	17.5	0.175	20	0.86		0.81
Ch. muritai	W2/4/1mur	17.5	0.145	6	0.9		0.86
Ch. muritai	W2/4/1mur	20	0.16	2	0.71		0.72
Ch. muritai	W2/4/1mur	25	0.175	12	1.16		0.97
Ch. muritai	W2/4/1mur	17.5	0.1475	4	0.9		0.72
Ch. muritai	W2/4/1mur	22.5	0.145	16	0.24		0.74
Ch. muritai	W2/4/1mur	25	0.132		0.24		0.89
Ch. muritai	W2/4/1mur	32.5	0.13		0.56		0.69
Ch. muritai	W2/4/1mur	30	0.109		1.05		0.7
Ch. muritai	W2/4/1mur	22.5	0.145		0.27		0.89
Ch. muritai	W2/4/1mur	25	0.15		1		0.81
Ch. muritai	W2/4/1mur	22.5	0.135		0.86		0.89
Ch. muritai	W2/4/1mur	22.5	0.123		1.07		0.82
Ch. muritai	W2/4/1mur	20	0.12		0.44		0.89
Ch. muritai	W2/6/4S	38	0.14	2	0.63	8	0.94
Ch. muritai	W2/6/4S	36.6	0.101	9	0.63	11	0.48
Ch. muritai	W2/6/4S	13	0.1125	15	0.97	3	1.04
Ch. muritai	W2/6/4S	32.5	0.141	12	0.58	5	0.9
Ch. muritai	W2/6/4S	26	0.145	14	0.51	13	0.85
Ch. muritai	W2/6/4S	36	0.135	10	0.73	2	0.86
Ch. muritai	W2/6/4S	34	0.131	9	0.37	3	0.9
Ch. muritai	W2/6/4S	21.5	0.115	5	0.31	15	0.83
Ch. muritai	W2/6/4S	21.5	0.122	2	0.4	13	1
Ch. muritai	W2/6/4S	25	0.121	10	0.54	4	0.7
Ch. muritai	W2/6/4S	50	0.111	5	0.75	13	0.86
Ch. muritai	W2/6/4S	22	0.125	9	0.9	8	0.97
Ch. muritai	W2/6/4S	27.5	0.125	4	0.39	14	0.98
Ch. muritai	W2/6/4S	28	0.133	8	0.54		0.79
Ch. muritai	W2/6/4S	15.4	0.144	11	0.56		0.54
Ch. muritai	W2/6/4S	19	0.135	5	0.56		0.89
Ch. muritai	W2/6/4S	25	0.115	19	0.5		0.87
Ch. muritai	W2/6/4S	28	0.135	9	0.77		0.61

Taxon	Accession	A	B	C	D	E	F
Ch. muritai	W2/6/4S	28	0.114	6	0.5		0.71
Ch. muritai	W2/6/4S	27.5	0.1253		0.75		0.79
Ch. muritai	W2/6/4S	19	0.112		0.47		1.04
Ch. muritai	W2/6/4S	17.5	0.112		1.91		0.78
Ch. muritai	W2/6/4S	22	0.136		0.44		0.78
Ch. muritai	W2/6/4S	20	0.153		0.72		0.82
Ch. muritai	W2/6/4S		0.128		0.52		0.6
Ch. muritai	W2/6/3	52	0.147	2	1.45	10	0.864
Ch. muritai	W2/6/3	35.5	0.143	4	1.027	2	0.864
Ch. muritai	W2/6/3	53.5	0.134	5	0.378	3	0.48
Ch. muritai	W2/6/3	53.5	0.126	21	0.567	6	0.77
Ch. muritai	W2/6/3	25.5	0.152	3	1.162	5	0.71
Ch. muritai	W2/6/3	30.9	0.167	16	0.432	12	0.527
Ch. muritai	W2/6/3	19.9	0.181	4	0.567	5	0.608
Ch. muritai	W2/6/3	58	0.131	9	0.662	12	0.797
Ch. muritai	W2/6/3	28	0.123	8	0.824	12	0.794
Ch. muritai	W2/6/3	21.8	0.121	4	0.135	5	0.87
Ch. muritai	W2/6/3	18	0.165	3	0.351	10	0.959
Ch. muritai	W2/6/3	21.6	0.148	5	0.821	13	0.743
Ch. muritai	W2/6/3	29.8	0.132	14	0.216	7	0.77
Ch. muritai	W2/6/3	17.2	0.164	27	0.337		0.702
Ch. muritai	W2/6/3	20.7	0.137	2	0.459		0.716
Ch. muritai	W2/6/3	16.5	0.126	10	0.797		0.945
Ch. muritai	W2/6/3	16.5	0.128	12	1.283		0.824
Ch. muritai	W2/6/3	23	0.118	3	0.229		0.81
Ch. muritai	W2/6/3	14	0.162		0.716		0.675
Ch. muritai	W2/6/3	21.4	0.132		0.513		0.716
Ch. muritai	W2/6/3	18.321	0.128		0.729		1.013
Ch. muritai	W2/6/3	21	0.131		0.216		0.702
Ch. muritai	W2/6/3	13.7	0.137		0.337		0.918
Ch. muritai	W2/6/3	48	0.116		0.473		0.783
Ch. muritai	W2/6/3	50	0.112		0.797		0.472
Ch. muritai	W2/6/3	18.7					1.04
Ch. muritai	W2/4/1S	46	0.151		0.391		1.067
Ch. muritai	W2/4/1S	46	0.125		0.5		0.702
Ch. muritai	W2/4/1S	21	0.155		0.67		0.931
Ch. muritai	W2/4/1S	15.2	0.154		0.58		1.108
Ch. muritai	W2/4/1S	36.2	0.127		0.689		1
Ch. muritai	W2/4/1S	17.8	0.127		0.189		0.702
Ch. muritai	W2/4/1S	26.3	0.147		0.621		0.797
Ch. muritai	W2/4/1S	18.5	0.104		1.5		0.854
Ch. muritai	W2/4/1S	43.5	0.123		0.297		0.905
Ch. muritai	W2/4/1S	37.7	0.141		0.81		0.905
Ch. muritai	W2/4/1S	15.8	0.147		0.56		0.837
Ch. muritai	W2/4/1S	54.7	0.162		0.689		0.972
Ch. muritai	W2/4/1S	31.5	0.175		0.85		0.729
Ch. muritai	W2/4/1S	26.5	0.157		0.2		0.966
Ch. muritai	W2/4/1S	40.7	0.098		0.87		0.892

Taxon	Accession	A	B	C	D	E	F
Ch. muritai	W2/4/1S	21.2	0.131		0.51		0.851
Ch. muritai	W2/4/1S	34.9	0.116		0.51		0.797
Ch. muritai	W2/4/1S	26.5	0.127		0.91		0.864
Ch. muritai	W2/4/1S	25.4	0.151		0.9		0.756
Ch. muritai	W2/4/1S	22	0.151		0.702		0.959
Ch. muritai	W2/4/1S	25.3	0.135		0.851		0.657
Ch. muritai	W2/4/1S	41.7	0.172		0.86		0.824
Ch. muritai	W2/4/1S	27.4	0.137		0.418		0.986
Ch. muritai	W2/4/1S	26.3	0.141		0.378		0.945
Ch. muritai	W2/4/1S	26.1	0.141		1.162		0.891
Ch. muritai	W2/4/1S	25.7	0.137		0.52		0.743
Ch. stevensonii	W1/6/4st	25	115	9	0.702	6	1.135
Ch. stevensonii	W1/6/4st	35	378	14	0.405	5	1.101
Ch. stevensonii	W1/6/4st	35	256	7	1.067	7	0.959
Ch. stevensonii	W1/6/4st	40	256	13	0.162	7	1.182
Ch. stevensonii	W1/6/4st	30	80	17	0.5	6	1.013
Ch. stevensonii	W1/6/4st	25	125	11	0.797	2	1.189
Ch. stevensonii	W1/6/4st	27.4	90	9	0.77	5	1.109
Ch. stevensonii	W1/6/4st	20	110	7	1.667	6	1.054
Ch. stevensonii	W1/6/4st	17.5	120	8	0.567	8	1.067
Ch. stevensonii	W1/6/4st	25	135	30	0.094	6	0.891
Ch. stevensonii	W1/6/4st	17.5	125	13	0.31	8	0.621
Ch. stevensonii	W1/6/4st	20	130	7	0.567	8	1.067
Ch. stevensonii	W1/6/4st	17.5	125	5	0.648	2	0.905
Ch. stevensonii	W1/6/4st	20	125	17	1.256	6	0.594
Ch. stevensonii	W1/6/4st	25	125	13	0.5	2	0.648
Ch. stevensonii	W1/6/4st	25	125	13	1.067	8	1.054
Ch. stevensonii	W1/6/4st	17.5	115		0.297	7	0.972
Ch. stevensonii	W1/6/4st	10	130		0.168	5	0.716
Ch. stevensonii	W1/6/4st	17.5	130		0.783	5	1.148
Ch. stevensonii	W1/6/4st	17.5	135		0.31	7	1.094
Ch. stevensonii	W1/6/4st	17.5	125		0.216	2	1.445
Ch. stevensonii	W1/6/4st	10	105		0.432	4	1.054
Ch. stevensonii	W1/6/4st	17.5	150		0.115	5	1.027
Ch. stevensonii	W1/6/4st	17.5	140		0.202	5	1.013
Ch. stevensonii	W1/6/4st	15	115		1.135		1.04
Ch. stevensonii	W1/6/5st	13.5	136	16	0.378	7	1.027
Ch. stevensonii	W1/6/5st	12.5	109	7	0.662	5	1.04
Ch. stevensonii	W1/6/5st	30	128	15	0.229	5	1.054
Ch. stevensonii	W1/6/5st	40	162	28	0.324	7	0.756
Ch. stevensonii	W1/6/5st	25	167	24	0.878	8	1.175
Ch. stevensonii	W1/6/5st	27.5	150	10	0.959	7	0.972
Ch. stevensonii	W1/6/5st	22.5	151	20	1.175	7	1.148
Ch. stevensonii	W1/6/5st	25	109	7	0.891	8	1.08
Ch. stevensonii	W1/6/5st	25	162	8	0.472	3	1.02
Ch. stevensonii	W1/6/5st	27.5	160	7	0.567	4	1.24
Ch. stevensonii	W1/6/5st	17.5	167	10	0.297	8	1.02
Ch. stevensonii	W1/6/5st	20	161	12	0.891	9	1.135

Taxon	Accession	A	B	C	D	E	F
Ch. stevensonii	W1/6/5st	22.5	148	9	0.432	7	1.108
Ch. stevensonii	W1/6/5st	22.5	106	25	0.175	8	1.283
Ch. stevensonii	W1/6/5st	20	161	14	0.797	6	1.013
Ch. stevensonii	W1/6/5st	25	151	17	0.486	6	1.148
Ch. stevensonii	W1/6/5st	15	166		0.229	5	1.108
Ch. stevensonii	W1/6/5st	12.5	152		0.283	7	0.905
Ch. stevensonii	W1/6/5st	15	177		0.554	6	1.01
Ch. stevensonii	W1/6/5st	10	155		1.27	4	1.02
Ch. stevensonii	W1/6/5st	20	151		0.864	2	1.06
Ch. stevensonii	W1/6/5st	17.5	116		0.54	4	1.06
Ch. stevensonii	W1/6/5st	12.5	109		0.716		1.162
Ch. stevensonii	W1/6/5st	20	100		0.378		1.17
Ch. stevensonii	W1/6/5st	17.5	120		0.783		1.05
N. carmichaeliae	Y2/4/3Scar		165	8	648	7	1168
N. carmichaeliae	Y2/4/3Scar		165	18	959	6	1060
N. carmichaeliae	Y2/4/3Scar		170	8	256	6	1120
N. carmichaeliae	Y2/4/3Scar		155	10	1080	9	810
N. carmichaeliae	Y2/4/3Scar		115	7	425	8	777
N. carmichaeliae	Y2/4/3Scar		150	11	472	5	993
N. carmichaeliae	Y2/4/3Scar		140	8	1108	2	1135
N. carmichaeliae	Y2/4/3Scar		120	29	1432	3	567
N. carmichaeliae	Y2/4/3Scar		160	1	250	12	824
N. carmichaeliae	Y2/4/3Scar		170	1	418	5	810
N. carmichaeliae	Y2/4/3Scar		150	28	716	14	1135
N. carmichaeliae	Y2/4/3Scar		140	12	567	6	837
N. carmichaeliae	Y2/4/3Scar		150	3	1108	10	979
N. carmichaeliae	Y2/4/3Scar		180	8	905		891
N. carmichaeliae	Y2/4/3Scar		140		486		878
N. carmichaeliae	Y2/4/3Scar		130		243		1067
N. carmichaeliae	Y2/4/3Scar		140		189		689
N. carmichaeliae	Y2/4/3Scar		140		175		851
N. carmichaeliae	Y2/4/3Scar		160		486		1080
N. carmichaeliae	Y2/4/3Scar		135		1135		918
N. carmichaeliae	Y2/4/3Scar		135		500		1090
N. carmichaeliae	Y2/4/3Scar		105		1391		970
N. carmichaeliae	Y2/4/3Scar		120		418		878
N. carmichaeliae	Y2/4/3Scar		105		1189		810
N. carmichaeliae	Y2/4/3Scar		125				1200
N. carmichaeliae	Y2/4/2S	65	163	20	459	9	743
N. carmichaeliae	Y2/4/2S	40	123	29	567	10	810
N. carmichaeliae	Y2/4/2S	35	152	3	243	2	560
N. carmichaeliae	Y2/4/2S	20	146	4	324	3	864
N. carmichaeliae	Y2/4/2S	30	145	15	1540	8	858
N. carmichaeliae	Y2/4/2S	15	154	32	432	4	709
N. carmichaeliae	Y2/4/2S	32.5	146	21	182	8	972
N. carmichaeliae	Y2/4/2S	52.5	144	2	297	10	979
N. carmichaeliae	Y2/4/2S	7.5	165	18	1200	9	837
N. carmichaeliae	Y2/4/2S	7.5	170	45	358	10	986

Taxon	Accession	A	B	C	D	E	F
N. carmichaeliae	Y2/4/2S	10	155	10	216	5	770
N. carmichaeliae	Y2/4/2S	17.5	161	5	810	14	1050
N. carmichaeliae	Y2/4/2S	10	161	19	608	11	1210
N. carmichaeliae	Y2/4/2S	12.5	161	37	864		878
N. carmichaeliae	Y2/4/2S	20	165		1370		1010
N. carmichaeliae	Y2/4/2S	27.5	169		459		979
N. carmichaeliae	Y2/4/2S	30	157		689		648
N. carmichaeliae	Y2/4/2S	20	166		418		959
N. carmichaeliae	Y2/4/2S	25	159		351		716
N. carmichaeliae	Y2/4/2S	25	151		648		216
N. carmichaeliae	Y2/4/2S	37.5	151		662		1060
N. carmichaeliae	Y2/4/2S	40	141		263		1135
N. carmichaeliae	Y2/4/2S	22.5	143		554		1320
N. carmichaeliae	Y2/4/2S	37.5	146		175		918
N. carmichaeliae	Y2/4/2S	40	124				986
N. carmichaeliae	Y2/41Scar	52	100	23	1243	7	1148
N. carmichaeliae	Y2/41Scar	50	115	9	506	2	878
N. carmichaeliae	Y2/41Scar	22.5	57	42	1580	2	824
N. carmichaeliae	Y2/41Scar	40	100	21	337	6	1067
N. carmichaeliae	Y2/41Scar	25	125	16	1350	4	918
N. carmichaeliae	Y2/41Scar	45	120	5	1120	6	959
N. carmichaeliae	Y2/41Scar	22.5	130	9	587	3	581
N. carmichaeliae	Y2/41Scar	17.5	87	15	860	2	594
N. carmichaeliae	Y2/41Scar	22.5	107	10	1090	7	1013
N. carmichaeliae	Y2/41Scar	17.5	82	8	1170	5	1020
N. carmichaeliae	Y2/41Scar	12.5	97	8	270	6	959
N. carmichaeliae	Y2/41Scar	45	145	11	837		1013
N. carmichaeliae	Y2/41Scar	22.5	100	4	608		824
N. carmichaeliae	Y2/41Scar	35	115	11	500		851
N. carmichaeliae	Y2/41Scar	22.5	125		283		837
N. carmichaeliae	Y2/41Scar	30	107		581		1090
N. carmichaeliae	Y2/41Scar	22.5	140		729		689
N. carmichaeliae	Y2/41Scar	22.5	140		500		864
N. carmichaeliae	Y2/41Scar	22.5	130		405		472
N. carmichaeliae	Y2/41Scar	17.5	125		405		716
N. carmichaeliae	Y2/41Scar	8.7	130		540		878
N. carmichaeliae	Y2/41Scar	20	90		594		986
N. carmichaeliae	Y2/41Scar	25	85		472		790
N. carmichaeliae	Y2/41Scar		155		540		621
N. carmichaeliae	Y2/41Scar				864		
C. willaimsii	C5/7/1S	30	150	4	391	7	1240
C. willaimsii	C5/7/1S	17.5	140	6	256	9	878
C. willaimsii	C5/7/1S	15	170	5	729	7	1148
C. willaimsii	C5/7/1S	30	155	10	729	6	986
C. willaimsii	C5/7/1S	25	125	10	216	2	1378
C. willaimsii	C5/7/1S	25	125	5	337	5	1540
C. willaimsii	C5/7/1S	17.5	130	6	554	3	1320
C. willaimsii	C5/7/1S	15	125	6	351	8	864

Taxon	Accession	A	B	C	D	E	F
C. willaimsii	C5/7/1S	30	135	2	351	5	756
C. willaimsii	C5/7/1S	30	135	5	945	8	1027
C. willaimsii	C5/7/1S	15	140		418	9	986
C. willaimsii	C5/7/1S	40	160		567		1067
C. willaimsii	C5/7/1S	45	165		324		608
C. willaimsii	C5/7/1S	40	160		148		986
C. willaimsii	C5/7/1S	45.5	124		554		1351
C. willaimsii	C5/7/1S	25	175		1000		1337
C. willaimsii	C5/7/1S	35	165		797		1081
C. willaimsii	C5/7/1S	35	155		797		905
C. willaimsii	C5/7/1S	45	150		256		1162
C. willaimsii	C5/7/1S	35	155		256		932
C. willaimsii	C5/7/1S	35	130		500		1067
C. willaimsii	C5/7/1S	35	115		337		1270
C. willaimsii	C5/7/1S	35	145		459		1283
C. willaimsii	C5/7/1S	25	127		1310		1202
C. willaimsii	C5/7/1S	30	125				1324
C. willaimsii	C5/6/1wil	40	115	8	716	4	1270
C. willaimsii	C5/6/1wil	37.5	139	5	1189	8	864
C. willaimsii	C5/6/1wil	42	156	3	2580	9	716
C. willaimsii	C5/6/1wil	30	166	7	432	9	918
C. willaimsii	C5/6/1wil	45	149	3	918	7	1081
C. willaimsii	C5/6/1wil	42.5	134	12	135	8	1310
C. willaimsii	C5/6/1wil	37.5	165	6	783	9	1013
C. willaimsii	C5/6/1wil	17.5	128	12	648	12	1486
C. willaimsii	C5/6/1wil	37.5	151	5	959	14	970
C. willaimsii	C5/6/1wil	35	145	2	675	11	1297
C. willaimsii	C5/6/1wil	35	142	4	837	11	1040
C. willaimsii	C5/6/1wil	27.5	145	16	1000	13	689
C. willaimsii	C5/6/1wil	40	179	3	1440		1405
C. willaimsii	C5/6/1wil	30	118	3	270		1270
C. willaimsii	C5/6/1wil	22.5	137		1135		1081
C. willaimsii	C5/6/1wil	22.5	142		1310		1297
C. willaimsii	C5/6/1wil	37.5	139		554		1027
C. willaimsii	C5/6/1wil	37.5	139		513		1175
C. willaimsii	C5/6/1wil	25	139		1980		932
C. willaimsii	C5/6/1wil	40	120		1210		1054
C. willaimsii	C5/6/1wil	40	129		310		1324
C. willaimsii	C5/6/1wil	32.5	128		189		729
C. willaimsii	C5/6/1wil	35	144		1310		1000
C. willaimsii	C5/6/1wil	30	149		1608		472
C. willaimsii	C5/6/1wil	50	104		1550		1202
C. willaimsii	C5/7/1Nwill	55	117	6	783	15	1135
C. willaimsii	C5/7/1Nwill	40	140	4	445	5	1351
C. willaimsii	C5/7/1Nwill	42.5	170	2	364	15	1310
C. willaimsii	C5/7/1Nwill	47.5	145	1	864	2	1290
C. willaimsii	C5/7/1Nwill	30	140	13	851	10	1364
C. willaimsii	C5/7/1Nwill	22.5	135	6	770	13	1440

Taxon	Accession	A	B	C	D	E	F
C. willaimsii	C5/7/1Nwill	45	137	6	756	11	1350
C. willaimsii	C5/7/1Nwill	35	120	15	851	3	1330
C. willaimsii	C5/7/1Nwill	40	107	8	337	12	1270
C. willaimsii	C5/7/1Nwill	30	120		283	14	945
C. willaimsii	C5/7/1Nwill	35	110		716	10	1350
C. willaimsii	C5/7/1Nwill	30	120		945	5	1310
C. willaimsii	C5/7/1Nwill	35	105		581		1250
C. willaimsii	C5/7/1Nwill	30	125		1910		1250
C. willaimsii	C5/7/1Nwill	30	135		310		1370
C. willaimsii	C5/7/1Nwill	45	105		1135		1520
C. willaimsii	C5/7/1Nwill	35	155		256		1320
C. willaimsii	C5/7/1Nwill	37	150		270		940
C. willaimsii	C5/7/1Nwill	22.5	145		324		590
C. willaimsii	C5/7/1Nwill	40	120		770		878
C. willaimsii	C5/7/1Nwill	32	145		216		918
C. willaimsii	C5/7/1Nwill	32	135		635		1240
C. willaimsii	C5/7/1Nwill	34	124		918		1229
C. willaimsii	C5/7/1Nwill	25	125		378		1480
C. willaimsii	C5/7/1Nwill	20	145		540		540
C. corrugata	C26/6/1	45	140	3	1797	7	1324
C. corrugata	C26/6/1	40	120	4	337	5	1283
C. corrugata	C26/6/1	15	135	1	608	6	1445
C. corrugata	C26/6/1	25	95	7	581	4	1567
C. corrugata	C26/6/1	30	105	23	1500	7	1581
C. corrugata	C26/6/1	30	105	2	1378	6	1337
C. corrugata	C26/6/1	22.5	135	20	2851	5	1108
C. corrugata	C26/6/1	30	165	28	1391	3	918
C. corrugata	C26/6/1	25	130	12	6891	14	851
C. corrugata	C26/6/1	35	110	3	3243	4	1540
C. corrugata	C26/6/1	30	125	4	932	2	1391
C. corrugata	C26/6/1	17.5	145	16	3040	5	1391
C. corrugata	C26/6/1	35	100	41	3243	7	1175
C. corrugata	C26/6/1	27.5	105			3	1027
C. corrugata	C26/6/1	25	130				1081
C. corrugata	C26/6/1	17.5	90				1081
C. corrugata	C26/6/1	15	125				1094
C. corrugata	C26/6/1	22.5	130				878
C. corrugata	C26/6/1	27.5	140				945
C. corrugata	C26/6/1	42.5	135				1162
C. corrugata	C26/6/1	42.5	145				648
C. corrugata	C26/6/1	40	200				1189
C. corrugata	C26/6/1	40	115				1378
C. corrugata	C26/6/1	15	130				1202
C. corrugata	C26/6/1	15	135				1297
C. corrugata	C26/6/2	32.5	210	2	581	4	1756
C. corrugata	C26/6/2	42.5	180	6	500	7	1148
C. corrugata	C26/6/2	30	85	16	175	5	1121
C. corrugata	C26/6/2	30	90	58	324	9	1662

Taxon	Accession	A	B	C	D	E	F
C. corrugata	C26/6/2	42.5	185	17	337	4	1256
C. corrugata	C26/6/2	22.5	140	2	486	6	1689
C. corrugata	C26/6/2	40	200	9	391	10	1554
C. corrugata	C26/6/2	37.5	195	12	540	6	1621
C. corrugata	C26/6/2	40	175	5	162	3	1797
C. corrugata	C26/6/2	30	180	3	202	8	1189
C. corrugata	C26/6/2	22.5	180	8	189	7	1459
C. corrugata	C26/6/2	20	155	11	756	2	2202
C. corrugata	C26/6/2	20	150	11	364	4	1270
C. corrugata	C26/6/2	15	140		229	4	1202
C. corrugata	C26/6/2		155		9243		1594
C. corrugata	C26/6/2		200		3405		1459
C. corrugata	C26/6/2		110		608		1243
C. corrugata	C26/6/2		315		337		1864
C. corrugata	C26/6/2		125		675		1716
C. corrugata	C26/6/2		120		10135		1594
C. corrugata	C26/6/2		110		8243		1540
C. corrugata	C26/6/2		155		1324		1635
C. corrugata	C26/6/2		185		4459		1918
C. corrugata	C26/6/2		120		3783		1351
C. corrugata	C26/6/2		115		4729		2310
C. corrugata	C26/6/3	17.5	163	8		2	2014
C. corrugata	C26/6/3	32.5	144	10		3	1675
C. corrugata	C26/6/3	30	191	7		3	932
C. corrugata	C26/6/3	25	165	7		10	1743
C. corrugata	C26/6/3	25	243	46		4	1675
C. corrugata	C26/6/3	37.5	149	10		4	1418
C. corrugata	C26/6/3	30	131	11		4	972
C. corrugata	C26/6/3	30	136	13		10	1310
C. corrugata	C26/6/3	20	212	12		7	1175
C. corrugata	C26/6/3	20	137	9		9	1135
C. corrugata	C26/6/3	32.5	177	7		8	1081
C. corrugata	C26/6/3		208	4		9	1108
C. corrugata	C26/6/3		169	3		16	1310
C. corrugata	C26/6/3		129	3			1283
C. corrugata	C26/6/3		151	25			1513
C. corrugata	C26/6/3		271	8			1251
C. corrugata	C26/6/3		186				1256
C. corrugata	C26/6/3		175				1621
C. corrugata	C26/6/3		179				1121
C. corrugata	C26/6/3		199				1054
C. corrugata	C26/6/3		197				1216
C. corrugata	C26/6/3		154				1756
C. corrugata	C26/6/3		143				1445
C. corrugata	C26/6/3		163				1175
C. corrugata	C26/6/3		198				1121
C. monroi	C31/6/1	32	60	7	1337	4	864
C. monroi	C31/6/1	17	60	32	364	4	878

Taxon	Accession	A	B	C	D	E	F
C. monroi	C31/6/1	17	93	5	581	3	945
C. monroi	C31/6/1	32	98	5	1357	2	905
C. monroi	C31/6/1	20	92	8	432	5	1054
C. monroi	C31/6/1	22	102	4	283	3	1445
C. monroi	C31/6/1	22	86	7	675	2	945
C. monroi	C31/6/1	12	73	8	810	5	1094
C. monroi	C31/6/1	25	124	25	513	4	716
C. monroi	C31/6/1	20	118	3	662	3	1283
C. monroi	C31/6/1	32	67	3	540	5	972
C. monroi	C31/6/1	20	74	2	324	4	716
C. monroi	C31/6/1	20	72	5	1283	5	702
C. monroi	C31/6/1	20	49	7	1000	5	878
C. monroi	C31/6/1	21	85	9	675	3	932
C. monroi	C31/6/1	25	76	1	297	5	1148
C. monroi	C31/6/1	17	106	19	486	5	1432
C. monroi	C31/6/1	15	130	11	608	3	1148
C. monroi	C31/6/1	25	93	7	567	3	1405
C. monroi	C31/6/1	20	117	19	364		1459
C. monroi	C31/6/1	22	117	4	513		1378
C. monroi	C31/6/1	20	102	4	418		1635
C. monroi	C31/6/1	30	102	10	810		1648
C. monroi	C31/6/1	20	89		662		986
C. monroi	C31/6/1		114		527		1486
C. monroi	C31/6/2	45	297	12	635	10	1189
C. monroi	C31/6/2	32	256	15	1081	2	1216
C. monroi	C31/6/2	15	283	29	2067	8	1662
C. monroi	C31/6/2	32	182	6	635	20	1513
C. monroi	C31/6/2	30	168	6	1351	22	945
C. monroi	C31/6/2	35	202	2	675	7	1675
C. monroi	C31/6/2	25	216	3	783	4	1540
C. monroi	C31/6/2	20	189	6	756	6	1594
C. monroi	C31/6/2	17	189	8	743	6	1081
C. monroi	C31/6/2	20	216	11	1135	7	1513
C. monroi	C31/6/2	40	202	120	689	11	1162
C. monroi	C31/6/2	20	243	7	1459	4	1716
C. monroi	C31/6/2	37	229	5	500	4	1216
C. monroi	C31/6/2	30	175	60	1554	5	986
C. monroi	C31/6/2	25	216	2	1067	12	1364
C. monroi	C31/6/2	40	202	40	202	12	1581
C. monroi	C31/6/2	37	135	37	1459	6	1310
C. monroi	C31/6/2	37	175	8	527	11	945
C. monroi	C31/6/2	30	222		1662	11	1608
C. monroi	C31/6/2	20	256		2662		1662
C. monroi	C31/6/2	20	229		824		1108
C. monroi	C31/6/2	25	182		527		662
C. monroi	C31/6/2	22	270		1094		1283
C. monroi	C31/6/2	25	202		878		1337
C. monroi	C31/6/2	22	216		1378		1405

Taxon	Accession	A	B	C	D	E	F
Co. crassicaule	P1/6/6N	21	100	60	432	6	1594
Co. crassicaule	P1/6/6N	24	90	68	716	9	1000
Co. crassicaule	P1/6/6N	10	125	30	986	7	743
Co. crassicaule	P1/6/6N	11	100	95	324	6	756
Co. crassicaule	P1/6/6N	13	125	36	567	3	851
Co. crassicaule	P1/6/6N	18	105	26	270	4	1067
Co. crassicaule	P1/6/6N	12	110	22	202	4	878
Co. crassicaule	P1/6/6N	9	105	95	200	5	1351
Co. crassicaule	P1/6/6N	21	115	21	1378	5	864
Co. crassicaule	P1/6/6N	11	130		567	4	918
Co. crassicaule	P1/6/6N	14.7	100		743	2	851
Co. crassicaule	P1/6/6N	21.4	75		1405	5	753
Co. crassicaule	P1/6/6N	9.7	115		256	6	486
Co. crassicaule	P1/6/6N	23.3	115		135	7	1031
Co. crassicaule	P1/6/6N	18.7	110		337		1094
Co. crassicaule	P1/6/6N	22.2	105		756		945
Co. crassicaule	P1/6/6N	17.3	125		500		1150
Co. crassicaule	P1/6/6N	8.2	105		864		1067
Co. crassicaule	P1/6/6N	7.8	130		297		837
Co. crassicaule	P1/6/6N	22.8	120		567		851
Co. crassicaule	P1/6/6N	15.8	95		40		1054
Co. crassicaule	P1/6/6N	12	115		567		1216
Co. crassicaule	P1/6/6N	12.4	135		1108		554
Co. crassicaule	P1/6/6N	13.2	120		891		891
Co. crassicaule	P1/6/6N	7.5	120		297		1054
Co. crassicaule	P1/6/2	16.7	128	8	770	8	970
Co. crassicaule	P1/6/2	13	114	80	851	7	910
Co. crassicaule	P1/6/2	14.5	131	27	405	37	640
Co. crassicaule	P1/6/2	11.8	154	38	662	9	780
Co. crassicaule	P1/6/2	19.3	90	41	337	7	940
Co. crassicaule	P1/6/2	15.4	136	75	2432	6	620
Co. crassicaule	P1/6/2	15.5	127	27	1148	8	590
Co. crassicaule	P1/6/2	18.6	146	63	1540	4	740
Co. crassicaule	P1/6/2	13.2	120	45	783	2	780
Co. crassicaule	P1/6/2	13.2	131		175	8	870
Co. crassicaule	P1/6/2	25.4	173		2486	2	770
Co. crassicaule	P1/6/2	19.7	140		835	3	630
Co. crassicaule	P1/6/2	13.1	127		932	10	700
Co. crassicaule	P1/6/2	19.9	132		337		950
Co. crassicaule	P1/6/2	17.5	150		554		870
Co. crassicaule	P1/6/2	13	113		1556		830
Co. crassicaule	P1/6/2	13	142		567		860
Co. crassicaule	P1/6/2	14.6	114		1108		770
Co. crassicaule	P1/6/2	11.1	143		202		890
Co. crassicaule	P1/6/2	17.7	112		491		540
Co. crassicaule	P1/6/2	16.9	104		824		890
Co. crassicaule	P1/6/2	9.4	117		743		850
Co. crassicaule	P1/6/2	14.3	136		486		870

Taxon	Accession	A	B	C	D	E	F
Co. crassicaule	P1/6/2	12.2	113		743		740
Co. crassicaule	P1/6/2	16.1	121				780
Co. crassicaule	P1/6/5	13.2	80	8	594	2	905
Co. crassicaule	P1/6/5	13.2	100	77	1027	4	689
Co. crassicaule	P1/6/5	15	85	26	972	6	810
Co. crassicaule	P1/6/5	17.4	115	64	743	7	445
Co. crassicaule	P1/6/5	16.3	90	43	500	8	445
Co. crassicaule	P1/6/5	11.65	110	24	1040	5	837
Co. crassicaule	P1/6/5	21.2	80	8	689	9	662
Co. crassicaule	P1/6/5	14.5	105	185	162	6	783
Co. crassicaule	P1/6/5	16	110	44	864	4	891
Co. crassicaule	P1/6/5	9.8	100		878	6	621
Co. crassicaule	P1/6/5	13.4	105		243	7	702
Co. crassicaule	P1/6/5	12.5	80		891	2	567
Co. crassicaule	P1/6/5	10.9	75		513	4	459
Co. crassicaule	P1/6/5	15.2	100		209	7	864
Co. crassicaule	P1/6/5	23.1	80		1324		783
Co. crassicaule	P1/6/5	20	85		1662		567
Co. crassicaule	P1/6/5	15.8	85		1256		527
Co. crassicaule	P1/6/5	9.5	110		1378		878
Co. crassicaule	P1/6/5	8.5	110		1371		1000
Co. crassicaule	P1/6/5	8.5	75		1243		730
Co. crassicaule	P1/6/5	16	120		1364		635
Co. crassicaule	P1/6/5	12.6	115		297		864
Co. crassicaule	P1/6/5	13.1	90		1310		716
Co. crassicaule	P1/6/5	12.3	105		621		554
Co. crassicaule	P1/6/5	14.2	75		878		716
C. nana	C24/6/1	35.9	100	19	1364	19	878
C. nana	C24/6/1	14.4	100	29	364	16	810
C. nana	C24/6/1	20.8	80	19	824	2	527
C. nana	C24/6/1	26.7	85	45	743	6	932
C. nana	C24/6/1	18.4	80	13	608	11	662
C. nana	C24/6/1	8.7	90	3	675	21	770
C. nana	C24/6/1	8.7	100	7	445	6	1001
C. nana	C24/6/1	8.7	95	4	918	3	1013
C. nana	C24/6/1	21.7	80	6	540	2	864
C. nana	C24/6/1	27.5	85	17	445	11	459
C. nana	C24/6/1	17.7	90	19	283	13	1054
C. nana	C24/6/1	26	95	34	662		1081
C. nana	C24/6/1	18.3	85	11	513		1013
C. nana	C24/6/1	26.3	96	24	216		635
C. nana	C24/6/1	21.5	105	2	810		1270
C. nana	C24/6/1	18.6	65	5	432		1366
C. nana	C24/6/1	9	110	20	797		1366
C. nana	C24/6/1	38.7	65	12	554		1364
C. nana	C24/6/1	15	110	6	405		986
C. nana	C24/6/1	18.6	105	10	1256		1027
C. nana	C24/6/1	14.1	95	12	581		905

Taxon	Accession	A	B	C	D	E	F
C. nana	C24/6/1	23.8	105		810		1094
C. nana	C24/6/1	20.5	97		986		905
C. nana	C24/6/1	17.1	73		567		1027
C. nana	C24/6/1	40.65	64		351		1135
C. nana	C24/7/3	17.75	116	10	405	3	945
C. nana	C24/7/3	12.9	104	24	256	3	864
C. nana	C24/7/3	17.1	116	7	405	5	905
C. nana	C24/7/3	14.7	137	22	378	3	972
C. nana	C24/7/3	13.1	114	6	324	4	837
C. nana	C24/7/3	16.8	104	1	229	4	1229
C. nana	C24/7/3	19.1	97	2	351	4	1202
C. nana	C24/7/3	7.35	112	1	324	3	810
C. nana	C24/7/3	13.4	108	10	459	2	1211
C. nana	C24/7/3	8.5	112	10	297	3	1283
C. nana	C24/7/3	18.7	94	5	121	2	1027
C. nana	C24/7/3	38.6	93	29	269		945
C. nana	C24/7/3	30.6	105	4	269		878
C. nana	C24/7/3	16.1	72	7	287		783
C. nana	C24/7/3	12.8	99	8	108		1216
C. nana	C24/7/3	10.7	109	6	294		1108
C. nana	C24/7/3	20.75	105	7	105		1013
C. nana	C24/7/3	14.7	127	14	148		1310
C. nana	C24/7/3	8.55	140	1	391		1189
C. nana	C24/7/3	15.55	115	14	256		959
C. nana	C24/7/3	16.2	122		148		1027
C. nana	C24/7/3	16.2	127		486		1189
C. nana	C24/7/3	23.95	119		310		1202
C. nana	C24/7/3	12.8	103		522		972
C. nana	C24/7/3	10.8	84		150		1256
C. nana	C24/7/1	20.4	82	15	324	6	1459
C. nana	C24/7/1	14.4	87	8	134	2	1045
C. nana	C24/7/1	18.3	79	15	337	4	1729
C. nana	C24/7/1	18.3	93	10	337	6	851
C. nana	C24/7/1	36.8	92	17	330	5	1229
C. nana	C24/7/1	24.2	101	23	225	4	1283
C. nana	C24/7/1	8	82	8	463	4	1351
C. nana	C24/7/1	22.9	74	5	477	4	513
C. nana	C24/7/1	14.7	100	50	310	5	959
C. nana	C24/7/1	23.1	95	9	181	3	1135
C. nana	C24/7/1	21.7	120	31	135	2	1067
C. nana	C24/7/1	15	104	34	513	5	1189
C. nana	C24/7/1	21.1	97	37	229		1108
C. nana	C24/7/1	17.3	89		278		1162
C. nana	C24/7/1	12.7	108		181		972
C. nana	C24/7/1	14	96		279		1621
C. nana	C24/7/1	30.5	84		244		1041
C. nana	C24/7/1	11.4	84		247		648
C. nana	C24/7/1	14	73		216		1513

Taxon	Accession	A	B	C	D	E	F
C. nana	C24/7/1	21.5	80		333		1135
C. nana	C24/7/1	8.5	90		304		1472
C. nana	C24/7/1	14.2	117		314		1067
C. nana	C24/7/1	17.1	105		247		1054
C. nana	C24/7/1	22.5	103		166		1243
C. nana	C24/7/1	18.6	82		99		1135
C. nana	C24/6/4	20.5			743		1094
C. nana	C24/6/4	10.2			365		959
C. nana	C24/6/4	15.6			186		972
C. nana	C24/6/4	18.7			214		1175
C. nana	C24/6/4	12.3			159		1121
C. nana	C24/6/4	18.2			668		945
C. nana	C24/6/4	18.2			174		1418
C. nana	C24/6/4	11.2			508		1202
C. nana	C24/6/4	19.9			347		837
C. nana	C24/6/4	9.8			797		1027
C. nana	C24/6/4	27.7			832		1000
C. nana	C24/6/4	15.6			233		1121
C. nana	C24/6/4	5.55			309		1081
C. nana	C24/6/4	10.6			305		1270
C. nana	C24/6/4	19.3			612		945
C. nana	C24/6/4	16.6			309		662
C. nana	C24/6/4	14.2			285		1216
C. nana	C24/6/4	12			556		581
C. nana	C24/6/4	20			418		1243
C. nana	C24/6/4	10.7			434		1081
C. nana	C24/6/4	14.45			270		851
C. nana	C24/6/4	18.8			300		986
C. nana	C24/6/4	24.8			544		1283
C. nana	C24/6/4	13.8			578		1081
C. nana	C24/6/4	18.2			433		1000
C. odorata	C4/7/1	66.7	129	7	1189	12	972
C. odorata	C4/7/1	50.7	132	13	621	11	824
C. odorata	C4/7/1	56.2	159	2	1445	11	662
C. odorata	C4/7/1	19.2	150	1	714	11	1216
C. odorata	C4/7/1	17.6	139	3	635	7	648
C. odorata	C4/7/1	14.5	132	11	824	9	864
C. odorata	C4/7/1	26.7	166	10	891	9	986
C. odorata	C4/7/1	33.5	118	10	1045	10	1108
C. odorata	C4/7/1	29.3	201	21	729	10	1081
C. odorata	C4/7/1	24	157	20	837	2	1175
C. odorata	C4/7/1	20.4	166	7	310	3	918
C. odorata	C4/7/1	30.2	152	3	851	9	1013
C. odorata	C4/7/1	25.4	136	4	770	11	1148
C. odorata	C4/7/1	37.45	161	5	351	3	1324
C. odorata	C4/7/1	17.9	152	6	648	2	932
C. odorata	C4/7/1	15.15	129	10	1554		1027
C. odorata	C4/7/1	13.35	169	3	810		608

Taxon	Accession	A	B	C	D	E	F
C. odorata	C4/7/1	14.95	169	8	608		1081
C. odorata	C4/7/1	20.9	148	1	418		1108
C. odorata	C4/7/1	18.1	150	3	472		1148
C. odorata	C4/7/1	35.3	164	1	689		405
C. odorata	C4/7/1	42.1	181	6	905		648
C. odorata	C4/7/1	59.05	151	12	797		1283
C. odorata	C4/7/1	66	137		675		797
C. odorata	C4/7/1	28	216		770		932
C. odorata	C4/6/2	54.8	195	2	280	4	1010
C. odorata	C4/6/2	38.8	185	5	702	5	1000
C. odorata	C4/6/2	38.8	150	20	972	4	986
C. odorata	C4/6/2	26	205	6	459	12	716
C. odorata	C4/6/2	57.1	155	1	256	7	851
C. odorata	C4/6/2	44.7	132	5	513	8	350
C. odorata	C4/6/2	17.9	147	4	824	12	878
C. odorata	C4/6/2	22.6	172	9	837	2	851
C. odorata	C4/6/2	26	174	2	1121	3	797
C. odorata	C4/6/2	35.6	166	9	581	9	332
C. odorata	C4/6/2	18.7	136	3	770	9	648
C. odorata	C4/6/2	24.3	167	5	1527	6	1108
C. odorata	C4/6/2	50.15	165	6	905	3	424
C. odorata	C4/6/2	42.9	173	7	405	10	1013
C. odorata	C4/6/2	40.6	197	13	797	8	1337
C. odorata	C4/6/2	53.7	164	12	1175	9	702
C. odorata	C4/6/2	45	166	1	1121	9	864
C. odorata	C4/6/2	45	155	5	824	4	702
C. odorata	C4/6/2	71.7	168	8	594		662
C. odorata	C4/6/2	22.3	200	8	797		770
C. odorata	C4/6/2	26	182	1	878		797
C. odorata	C4/6/2	31.65	150	10	972		986
C. odorata	C4/6/2	33.15	159	17	648		1040
C. odorata	C4/6/2	19.7	152		594		1229
C. odorata	C4/6/2	23.65	200		1148		1121
C. compacta	C32/6/1	37	134	5	621	6	660
C. compacta	C32/6/1	14.5	161	5	1445	7	905
C. compacta	C32/6/1	30.25	136	23	714	5	1045
C. compacta	C32/6/1	39.5	127	6	635	7	585
C. compacta	C32/6/1	27.8	113	4	824	4	950
C. compacta	C32/6/1	37.4	86	33	891	6	1090
C. compacta	C32/6/1	32.5	73	2	1045	5	1125
C. compacta	C32/6/1	28.5	67	12	729	6	960
C. compacta	C32/6/1	41.95	112	23	837	6	986
C. compacta	C32/6/1	34.4	131	29	310	7	665
C. compacta	C32/6/1	18.1	115	8	851	3	890
C. compacta	C32/6/1	22.45	88	13	770	2	790
C. compacta	C32/6/1	37.55	104	67	351	8	885
C. compacta	C32/6/1	31.85	94	14	648	8	925
C. compacta	C32/6/1	20.5	134	46	1554	3	700

Taxon	Accession	A	B	C	D	E	F
C. compacta	C32/6/1	25.15	83		810	4	1200
C. compacta	C32/6/1	27.45	104		608		905
C. compacta	C32/6/1	17.8	142		418		675
C. compacta	C32/6/1	20.95	96		472		750
C. compacta	C32/6/1	19.3	103		689		550
C. compacta	C32/6/1	16.2	83		905		735
C. compacta	C32/6/1	16.3	126		797		840
C. compacta	C32/6/1	44.3	135		675		880
C. compacta	C32/6/1	35.95	131		770		830
C. compacta	C32/6/1	33.2	139		280		600
C. compacta	C32/7/3	36.1	112	18	702	12	340
C. compacta	C32/7/3	24.4	110	4	972	5	740
C. compacta	C32/7/3	35.5	103	34	459	8	870
C. compacta	C32/7/3	15.5	135	24	256	11	605
C. compacta	C32/7/3	23.6	155	5	513	9	440
C. compacta	C32/7/3	19.25	79	42	824	9	800
C. compacta	C32/7/3	37.2	79	3	837	2	510
C. compacta	C32/7/3	37.2	97	2	1121	4	690
C. compacta	C32/7/3	30.55	97	11	581	7	550
C. compacta	C32/7/3	22.4	83	3	770	4	395
C. compacta	C32/7/3	17.75	57	1	1527	10	475
C. compacta	C32/7/3	30.6	76	10	905	5	620
C. compacta	C32/7/3	25.1	139	10	405	5	370
C. compacta	C32/7/3	45.35	144	13	797	19	450
C. compacta	C32/7/3	16.8	110	41	1175	2	590
C. compacta	C32/7/3	29.45	82	4	1121	7	395
C. compacta	C32/7/3	24.75	113	2	824	13	545
C. compacta	C32/7/3	40.5	145	6	594	7	510
C. compacta	C32/7/3	25.6	121	15	797		565
C. compacta	C32/7/3	18.25	110	10	878		645
C. compacta	C32/7/3	37.3	101		972		685
C. compacta	C32/7/3	52.25	99		648		565
C. compacta	C32/7/3	38.1	110		594		690
C. compacta	C32/7/3	13.35	110		1148		435
C. compacta	C32/7/3	27.1	88		580		525
C. petriei	C20/7/4	44.8	90	9	986	10	743
C. petriei	C20/7/4	12.8	95	15	1175	11	395
C. petriei	C20/7/4	26.9	92	33	635	9	891
C. petriei	C20/7/4	26.9	85	11	689	8	567
C. petriei	C20/7/4	16.4	100	5	472	9	702
C. petriei	C20/7/4	36.8	85	2	554	12	824
C. petriei	C20/7/4	24.5	87	10	635	2	500
C. petriei	C20/7/4	37	90	11	824	4	878
C. petriei	C20/7/4	21.5	85	11	729	9	797
C. petriei	C20/7/4	12.7	90	11	162		1148
C. petriei	C20/7/4	27.6	100	23	445		1135
C. petriei	C20/7/4	17.6	60	18	1486		1000
C. petriei	C20/7/4	13.6	100		810		1135

Taxon	Accession	A	B	C	D	E	F
C. petriei	C20/7/4	13.1	98		108		864
C. petriei	C20/7/4	10.7	95		581		1283
C. petriei	C20/7/4	13.4	97		1210		729
C. petriei	C20/7/4	4.91	105		905		662
C. petriei	C20/7/4	2.86	60		283		743
C. petriei	C20/7/4	23	55		797		824
C. petriei	C20/7/4	16.2	75		148		1256
C. petriei	C20/7/4	54.6	73		378		932
C. petriei	C20/7/4	4.36	107		297		1013
C. petriei	C20/7/4	44.9	95		1486		1121
C. petriei	C20/7/4	17.2	78		324		986
C. petriei	C20/7/4	20	96		540		1175
C. petriei	C20/7/5	21.7	107	4	635	12	918
C. petriei	C20/7/5	18.5	115	15	202	10	743
C. petriei	C20/7/5	11.9	100	7	324	13	959
C. petriei	C20/7/5	14.8	125	5	189	10	945
C. petriei	C20/7/5	14.8	105	18	432	6	1054
C. petriei	C20/7/5	23.6	100	6	472	3	1000
C. petriei	C20/7/5	17.6	100	33	297	18	1009
C. petriei	C20/7/5	23.7	120	6	445	14	743
C. petriei	C20/7/5	32.4	110	10	675	13	891
C. petriei	C20/7/5	31.4	65	3	716	14	810
C. petriei	C20/7/5	20.6	100	10	1135	8	918
C. petriei	C20/7/5	27	100	25	972	12	810
C. petriei	C20/7/5	16.6	100	9	2243		864
C. petriei	C20/7/5	30	100	20	891		662
C. petriei	C20/7/5	21.6	115	26	648		675
C. petriei	C20/7/5	13.2	110	50	594		986
C. petriei	C20/7/5	15.3	109		148		845
C. petriei	C20/7/5	20.2	96		324		500
C. petriei	C20/7/5	30.3	108		445		918
C. petriei	C20/7/5	27.9	98		270		662
C. petriei	C20/7/5	14.3	85		472		878
C. petriei	C20/7/5	11.6	110		297		905
C. petriei	C20/7/5	11.5	75		1148		783
C. petriei	C20/7/5	24.2	90		1189		1000
C. petriei	C20/7/5	24.2	140		635		824
C. petriei	C20/7/6	51.3	95	32	783	11	918
C. petriei	C20/7/6	33	88	47	662	13	824
C. petriei	C20/7/6	25	85	13	459	9	1027
C. petriei	C20/7/6	24.8	98	18	540	16	1054
C. petriei	C20/7/6	31.4	94	5	378	4	972
C. petriei	C20/7/6	24.9	114	17	202	19	1027
C. petriei	C20/7/6	16.3	79	10	527	11	743
C. petriei	C20/7/6	13.8	93	59	418	15	986
C. petriei	C20/7/6	21.4	103	9	445	9	1148
C. petriei	C20/7/6	17.7	113	18	472	6	743
C. petriei	C20/7/6	17.7	108	60	486		864

Taxon	Accession	A	B	C	D	E	F
C. petriei	C20/7/6	12.7	89	16	419		1081
C. petriei	C20/7/6	15.7	118	17	486		1040
C. petriei	C20/7/6	18.6	100	43	567		1202
C. petriei	C20/7/6	12.9	67		364		743
C. petriei	C20/7/6	12	87		364		851
C. petriei	C20/7/6	14	102		432		945
C. petriei	C20/7/6	12.8	123		567		743
C. petriei	C20/7/6	8.3	82		445		675
C. petriei	C20/7/6	20.3	86		540		716
C. petriei	C20/7/6	25.9	98		486		932
C. petriei	C20/7/6	15.1	138		743		945
C. petriei	C20/7/6	9	99		527		932
C. petriei	C20/7/6	19.6	79		418		824
C. petriei	C20/7/6		79		100		972
N. torulosum	Y1/6/3	50.7	135	9	837	4	1000
N. torulosum	Y1/6/3	29.2	115	14	851	10	567
N. torulosum	Y1/6/3	44.8	125	4	662	3	621
N. torulosum	Y1/6/3	26.4	125	9	270	7	1108
N. torulosum	Y1/6/3	17.7	130	22	1027	8	945
N. torulosum	Y1/6/3	29.05	130	14	554	2	1121
N. torulosum	Y1/6/3	29.1	145	9	716	6	1135
N. torulosum	Y1/6/3	17.8	130	19	837	9	959
N. torulosum	Y1/6/3	17.9	135	13	229	9	824
N. torulosum	Y1/6/3	9.2	125	2	783	7	972
N. torulosum	Y1/6/3	17.5	140	6	391	8	878
N. torulosum	Y1/6/3	14.2	115		1045	5	1094
N. torulosum	Y1/6/3	18.3	133		337	7	905
N. torulosum	Y1/6/3	18.3	110		310	5	1067
N. torulosum	Y1/6/3	18.2	155		689		1405
N. torulosum	Y1/6/3	16.8	115		891		959
N. torulosum	Y1/6/3	16.9	145		364		864
N. torulosum	Y1/6/3	14.7	135		716		1027
N. torulosum	Y1/6/3	18.6	80		702		1148
N. torulosum	Y1/6/3	15.6	90		324		1081
N. torulosum	Y1/6/3	22.3	120		297		1094
N. torulosum	Y1/6/3	18.5	150		567		932
N. torulosum	Y1/6/3	33.5	145		608		932
N. torulosum	Y1/6/3	24.7	115		283		1027
N. torulosum	Y1/6/3	17.1	125		783		1081
N. torulosum	Y1/6/4	49.3	114	6	418	5	729
N. torulosum	Y1/6/4	28.9	107	27	594	2	851
N. torulosum	Y1/6/4	23.6	99	39	1121	7	770
N. torulosum	Y1/6/4	15.1	124	19	918	8	743
N. torulosum	Y1/6/4	13.4	131	25	675	9	824
N. torulosum	Y1/6/4	16.5	127	10	810	5	972
N. torulosum	Y1/6/4	41.75	100	21	810	8	635
N. torulosum	Y1/6/4	23.1	121	16	459	8	756
N. torulosum	Y1/6/4	23	100	24	270	9	716

Taxon	Accession	A	B	C	D	E	F
N. torulosum	Y1/6/4	44.35	89	24	135	4	837
N. torulosum	Y1/6/4	44.5	124	19	243	7	824
N. torulosum	Y1/6/4	41.4	111	15	472	9	662
N. torulosum	Y1/6/4	22.9	133	20	513		689
N. torulosum	Y1/6/4	32.8	87	7	743		756
N. torulosum	Y1/6/4	21.6	94	20	972		743
N. torulosum	Y1/6/4	16	86	24	837		891
N. torulosum	Y1/6/4	12.8	100		743		878
N. torulosum	Y1/6/4	22.1	99		837		689
N. torulosum	Y1/6/4	11.3	70		837		594
N. torulosum	Y1/6/4	15.3	100		743		824
N. torulosum	Y1/6/4	15.4	89		554		648
N. torulosum	Y1/6/4	15.5	132		445		513
N. torulosum	Y1/6/4	19.3	100		472		581
N. torulosum	Y1/6/4	23.2	102		472		608
N. torulosum	Y1/6/4				716		702
N. torulosum	Y1/6/5	49.2	120	8	1136	9	878
N. torulosum	Y1/6/5	29.4	95	16	702	11	1067
N. torulosum	Y1/6/5	29.4	110	11	1418	7	783
N. torulosum	Y1/6/5	47.4	135	12	594	4	878
N. torulosum	Y1/6/5	58.7	140	3	1337	10	1027
N. torulosum	Y1/6/5	40.8	140	13	202	3	783
N. torulosum	Y1/6/5	24.5	98	16	1108	8	959
N. torulosum	Y1/6/5	19.3	130	26	283	17	837
N. torulosum	Y1/6/5	26.6	120	28	1054	10	824
N. torulosum	Y1/6/5	15.3	100	15	918	10	1054
N. torulosum	Y1/6/5	16.8	110	34	1135	4	1013
N. torulosum	Y1/6/5	14.5	103	20	432	11	635
N. torulosum	Y1/6/5	11.4	140	28	1000	8	824
N. torulosum	Y1/6/5	27.45	140		878		1094
N. torulosum	Y1/6/5	19.4	125		310		986
N. torulosum	Y1/6/5	24.5	135		567		675
N. torulosum	Y1/6/5	27.7	150		1540		702
N. torulosum	Y1/6/5	22.95	128		594		1000
N. torulosum	Y1/6/5	25.85	125		1000		878
N. torulosum	Y1/6/5	34.05	130		540		945
N. torulosum	Y1/6/5	37	120		1000		797
N. torulosum	Y1/6/5	28.25	110		1040		810
N. torulosum	Y1/6/5	24.3	95		297		770
N. torulosum	Y1/6/5	54.2	120		189		797
N. torulosum	Y1/6/5	48	100		338		918
N. glabrescens	Y/4/1	40.3	115	6	1135	8	1148
N. glabrescens	Y/4/1	35.6	110	3	716	5	945
N. glabrescens	Y/4/1	23.8	145	1	459	5	1121
N. glabrescens	Y/4/1	12.8	150	2	405	9	1027
N. glabrescens	Y/4/1	46.9	110	3	270	12	810
N. glabrescens	Y/4/1	24.2	105	10	1310	5	581
N. glabrescens	Y/4/1	37.1	115	13	756	7	945

Taxon	Accession	A	B	C	D	E	F
N. glabrescens	Y/4/1	30.8	125	3	1216	9	1000
N. glabrescens	Y/4/1	49.1	100	13	1283		1067
N. glabrescens	Y/4/1	46.2	120	9	837		1081
N. glabrescens	Y/4/1	19	120	15	689		864
N. glabrescens	Y/4/1	42.1	115	19	2756		1027
N. glabrescens	Y/4/1	41.3	135	12	1513		1094
N. glabrescens	Y/4/1	44.3	135		378		1094
N. glabrescens	Y/4/1	27.3	125		635		1148
N. glabrescens	Y/4/1	31.2	110		1405		1135
N. glabrescens	Y/4/1	32.8	130		527		851
N. glabrescens	Y/4/1	32.4	110		513		1094
N. glabrescens	Y/4/1	16.2	125		932		810
N. glabrescens	Y/4/1	21.8	130		527		782
N. glabrescens	Y/4/1	35.8	120		648		770
N. glabrescens	Y/4/1	25	125		472		716
N. glabrescens	Y/4/1	22.1	105		500		513
N. glabrescens	Y/4/1	35.4	135		635		1013
N. glabrescens	Y/4/1	20.6	130		716		1040
N. glabrescens	Y/6/3	58.5	130	9	1189	6	743
N. glabrescens	Y/6/3	38.9	95	14	635	2	824
N. glabrescens	Y/6/3	26.7	125	10	1256	8	891
N. glabrescens	Y/6/3	36.5	96	10	324	3	972
N. glabrescens	Y/6/3	36.2	140	8	635	2	986
N. glabrescens	Y/6/3	20.1	140	22	594	9	824
N. glabrescens	Y/6/3	29.45	100	7	770	3	973
N. glabrescens	Y/6/3	8.5	110	61	486	11	972
N. glabrescens	Y/6/3	31.75	100	22	486	9	689
N. glabrescens	Y/6/3	23.45	110	13	445		743
N. glabrescens	Y/6/3	16.8	115	7	635		1216
N. glabrescens	Y/6/3	12.7	115		472		1297
N. glabrescens	Y/6/3	28.55	110		675		945
N. glabrescens	Y/6/3	27.7	100		1000		878
N. glabrescens	Y/6/3	16	135		445		1108
N. glabrescens	Y/6/3	19.7	155		594		864
N. glabrescens	Y/6/3	15.2	100		527		1216
N. glabrescens	Y/6/3	25.7	100		635		1216
N. glabrescens	Y/6/3	26.5	110		540		1108
N. glabrescens	Y/6/3	25.3	110		621		972
N. glabrescens	Y/6/3	27.4	100		836		878
N. glabrescens	Y/6/3	19.9	110		945		810
N. glabrescens	Y/6/3	16.2	125		1648		945
N. glabrescens	Y/6/3	50.9	105		472		675
N. glabrescens	Y/6/3	24.35	100		621		743
N. glabrescens	Y/6/4	58.9	115	15	554	10	1040
N. glabrescens	Y/6/4	54.5	75	25	324	8	635
N. glabrescens	Y/6/4	73.4	120	9	621	3	1013
N. glabrescens	Y/6/4	53.9	115	17	243	7	851
N. glabrescens	Y/6/4	12.8	125	9	351	12	648

Taxon	Accession	A	B	C	D	E	F
N. glabrescens	Y/6/4	41	120	17	581	15	1135
N. glabrescens	Y/6/4	22.8	120	4	310	10	824
N. glabrescens	Y/6/4	40.65	125	27	486	9	445
N. glabrescens	Y/6/4	30.4	105	37	283	10	824
N. glabrescens	Y/6/4	22.7	120	5	324	12	918
N. glabrescens	Y/6/4	32.6	100	23	162	15	1000
N. glabrescens	Y/6/4	26.4	105		675	12	1000
N. glabrescens	Y/6/4	25.5	125		554		716
N. glabrescens	Y/6/4	31.9	125		500		716
N. glabrescens	Y/6/4	24.7	95		324		810
N. glabrescens	Y/6/4	16.8	90		621		1094
N. glabrescens	Y/6/4	14.5	135		662		918
N. glabrescens	Y/6/4	15.5	90		189		918
N. glabrescens	Y/6/4	20.5	145		405		905
N. glabrescens	Y/6/4	29.2	140		405		648
N. glabrescens	Y/6/4	22.1	110		432		878
N. glabrescens	Y/6/4	24.5	110		486		594
N. glabrescens	Y/6/4	65.1	105		472		837
N. glabrescens	Y/6/4	29	120		229		891
N. glabrescens	Y/6/4	18.9	120		202		905
N. glabrescens	Y/6/2	20.8	135	16	1094	11	905
N. glabrescens	Y/6/2	15.9	135	2	810	3	959
N. glabrescens	Y/6/2	12.8	145	5	297	8	1000
N. glabrescens	Y/6/2	19.5	125	4	243	6	824
N. glabrescens	Y/6/2	21.1	125	6	283	6	1094
N. glabrescens	Y/6/2	17.9	95	16	270	10	932
N. glabrescens	Y/6/2	15	105	19	418	12	837
N. glabrescens	Y/6/2	13.6	140	16	418	5	743
N. glabrescens	Y/6/2	34.1	135	8	864	7	1000
N. glabrescens	Y/6/2	40.5	135	18	445	8	905
N. glabrescens	Y/6/2	33.7	80	16	486	10	783
N. glabrescens	Y/6/2	56.4	100		391	5	919
N. glabrescens	Y/6/2	33	125		432		1229
N. glabrescens	Y/6/2	31.2	130		162		1108
N. glabrescens	Y/6/2	57.45	110		810		1000
N. glabrescens	Y/6/2	44	155		797		918
N. glabrescens	Y/6/2	32.7	110		418		878
N. glabrescens	Y/6/2	26.9	90		554		1189
N. glabrescens	Y/6/2	12.45	105		1013		1013
N. glabrescens	Y/6/2	12.5	145		513		648
N. glabrescens	Y/6/2	15.3	150		432		972
N. glabrescens	Y/6/2	12.8	125		972		837
N. glabrescens	Y/6/2	13.1	115		283		918
N. glabrescens	Y/6/2	12.5	115		189		945
N. glabrescens	Y/6/2		130		581		918
C. australis	C16/6/2	42.9	105	21	1000	14	824
C. australis	C16/6/2	35.5	140	8	945	9	1054
C. australis	C16/6/2	33.8	135	17	810	12	878

Taxon	Accession	A	B	C	D	E	F
C. australis	C16/6/2	47.6	115	2	1162	3	878
C. australis	C16/6/2	31	125	9	297	11	905
C. australis	C16/6/2	36.4	130	4	310	5	1121
C. australis	C16/6/2	13.1	135	2	500	4	837
C. australis	C16/6/2	11.2	125	9	581	7	770
C. australis	C16/6/2	13.8	120	4	702	4	864
C. australis	C16/6/2	29.5	140	2	175	9	783
C. australis	C16/6/2	31.2	85	15	581		1013
C. australis	C16/6/2	36.1	115	8	351		918
C. australis	C16/6/2	38.6	110	22	635		1121
C. australis	C16/6/2	19.6	105	55	729		878
C. australis	C16/6/2	17.8	120		540		662
C. australis	C16/6/2	27.1	95		540		1027
C. australis	C16/6/2	35	150		189		743
C. australis	C16/6/2	32.55	125		297		770
C. australis	C16/6/2	27.7	120		851		810
C. australis	C16/6/2	23.1	100		1189		905
C. australis	C16/6/2	23	145		783		918
C. australis	C16/6/2	20	115		189		1000
C. australis	C16/6/2	13.8	100		189		743
C. australis	C16/6/2	26.4	140		405		918
C. australis	C16/6/2	25.5	130		1378		837
C. australis	C16/6/3N	38	110	15	1027	7	1202
C. australis	C16/6/3N	38.4	135	40	1405	3	1081
C. australis	C16/6/3N	40.5	155	3	756	5	810
C. australis	C16/6/3N	26.1	160	20	1905	4	810
C. australis	C16/6/3N	40.1	160	10	810	7	1081
C. australis	C16/6/3N	33.1	130	7	175	10	1081
C. australis	C16/6/3N	33.7	145	23	1594	8	1364
C. australis	C16/6/3N	17.6	135	11	189	8	1000
C. australis	C16/6/3N	23.9	150	43	987	9	1391
C. australis	C16/6/3N	39.1	130	12	364	2	1013
C. australis	C16/6/3N	22.55	145	9	770	6	1283
C. australis	C16/6/3N	30.3	145		2216	5	1162
C. australis	C16/6/3N	25.3	145		594	10	945
C. australis	C16/6/3N	35.8	170		216		1000
C. australis	C16/6/3N	42	125		1500		1472
C. australis	C16/6/3N	34	150		824		945
C. australis	C16/6/3N	23.2	130		1351		1121
C. australis	C16/6/3N	25.8	145		243		1148
C. australis	C16/6/3N	48.7	130		810		581
C. australis	C16/6/3N	31.55	110		445		1121
C. australis	C16/6/3N	33.3	140		594		1000
C. australis	C16/6/3N	20.9	150		702		1162
C. australis	C16/6/3N	24.8	155		459		1081
C. australis	C16/6/3N	12.1	180		810		986
C. australis	C16/6/3N	25.1	160		945		1189
C. australis	C16/6/3S	35.6	150	10	1837	11	1027

Taxon	Accession	A	B	C	D	E	F
C. australis	C16/6/3S	24.7	155	35	837	12	1243
C. australis	C16/6/3S	29.3	150	3	1135	2	1067
C. australis	C16/6/3S	20.3	95	9	864	6	1162
C. australis	C16/6/3S	37.5	170	29	635	12	932
C. australis	C16/6/3S	34.7	160		770	4	1351
C. australis	C16/6/3S	29.9	150		1054	5	851
C. australis	C16/6/3S	25.3	145		782	10	1243
C. australis	C16/6/3S	28.8	150		554	8	1391
C. australis	C16/6/3S	34.8	155		716	10	864
C. australis	C16/6/3S	29.7	160		1445	2	1054
C. australis	C16/6/3S	18.2	150		1243		1324
C. australis	C16/6/3S	20	145		635		1148
C. australis	C16/6/3S	22.9	120		594		1229
C. australis	C16/6/3S	14.5	135		891		1527
C. australis	C16/6/3S	32.6	150		1189		851
C. australis	C16/6/3S	23.3	120		864		1135
C. australis	C16/6/3S	16.6	150		1067		945
C. australis	C16/6/3S	17.9	150		1270		756
C. australis	C16/6/3S	21.6	165		878		837
C. australis	C16/6/3S	16.55	85		594		1054
C. australis	C16/6/3S	27.25	175		432		1135
C. australis	C16/6/3S	19.2	165		1081		1081
C. australis	C16/6/3S	31.3	140		405		1081
C. australis	C16/6/3S	21.1	135		662		

Appendix 4 Terminal taxa used for the phylogenetic study (Chapter 6).

Species	Origin	Herbarium vouchers
Astragalus bisulcatus (Hook.) Gray	North America	CHR 409846
Biserrula pelecinus L.	Mediterranean, Nth Africa	CHR 434942, 166186
Carmichaelia appressa G.Simpson	New Zealand	CHR 257870, 496552
Carmichaelia arborea (G.Forst.) Druce	New Zealand	CHR 45682
Carmichaelia astonii G.Simpson	New Zealand	CHR 277521, 279271
Carmichaelia australis R.Br.	New Zealand	CHR 496553, 497354
Carmichaelia compacta Petrie	New Zealand	CHR 496515, 496560
Carmichaelia corrugata Colenso	New Zealand	CHR 496554, 496555, 497358
Carmichaelia curta Petrie	New Zealand	CHR 284602, 508033
Carmichaelia exsul F.Muell.	Lord Howe Island	CHR 45526a/b, 45527a, 335260, 338019, 500961, 502471a
Carmichaelia hollowayi G.Simpson	New Zealand	CHR 506438
Carmichaelia juncea Hook.f.	New Zealand	CHR 45811b, 213064
Carmichaelia kirkii Hook.f.	New Zealand	CHR 421347, 499501, 500290
Carmichaelia monroi Hook.f.	New Zealand	CHR 497355, 497356

Appendix 4 continued

Species	Origin	Herbarium vouchers
Carmichaelia nana (Hook.f.) Hook.f.	New Zealand	CHR 496572, 496577, 497353, 497357
Carmichaelia odorata Benth.	New Zealand	CHR 497359, 496605
Carmichaelia petriei Kirk	New Zealand	CHR 496574, 496575, 496576
Carmichaelia uniflora Kirk	New Zealand	CHR 314469b, 497334
Carmichaelia vexillata Heenan	New Zealand	CHR 54250b
Carmichaelia williamsii Kirk	New Zealand	CHR 496563, 496606
Chordospartium muritai A.W.Purdie	New Zealand	CHR 496561, 496607, 496608
Chordospartium stevensonii Cheeseman	New Zealand	CHR 472348, 497371, 497372
Clianthus puniceus (G.Don) Sol. ex Lindl.	New Zealand	CHR 397764, 500558
Corallospartium crassicaule (Hook.f.) J.B.Armstr.	New Zealand	CHR 496569, 496578, 496579
Lessertia perennans DC.	Sth Africa	CHR 144976
Notospartium carmichaeliae Hook.f.	New Zealand	CHR 500703, 496609, 496611
Notospartium glabrescens Petrie	New Zealand	CHR 78930, 279196

Appendix 4 continued

Species	Origin	Herbarium vouchers
Notospartium torulosum Kirk	New Zealand	CHR 496562, 496612, 496613
Sutherlandia frutescens R.Br.	Sth Africa	CHR 92180a/b, 147993, 353451
Swainsona cyclocarpa F.Muell.	Australia	NSW 388002
Swainsona decurrens A.Lee	Australia	NSW 246787
Swainsona formosa (G.Don) J.Thompson	Australia	CHR 126387; NSW 221202
Swainsona galegifolia (Andr.) R.Br.	Australia	CHR 83529a/b; NSW 231841, 275183
Swainsona kingii F.Muell.	Australia	NSW 395565
Swainsona lessertiifolia DC.	Australia	CHR 429748
Swainsona microphylla A.Gray	Australia	CHR 411166a, 411178a
Swainsona novae-zelandiae Hook.f.	New Zealand	CHR 496615, 496616
Swainsona oligophylla F.Muell. ex Benth.	Australia	CHR 429750
Swainsona oroboides F.Muell. ex Benth.	Australia	CHR 72918, 452096
Swainsona recta A.Lee	Australia	NSW 213408
Swainsona stipularis F.Muell.	Australia	CHR 172905, 429747

Appendix 4 continued

Species	Origin	Herbarium vouchers
Swainsona swainsonioides (Benth.) A.Lee ex J.Black	Australia	CHR 429742a/b

Appendix 5 Data matrix for the phylogenetic analysis (Chapter 6).

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Astragalus bisulcatus	0	0	?	0	?	0	0	0
Biserrula pelecinus	0	0	?	0	?	0	0	0
Carmichaelia appressa	1	0	3	1	0	1	1	1
Carmichaelia arborea	1	0	3	1	0	1	[01]	1
Carmichaelia astonii	2	0	0	1	0	2	1	1
Carmichaelia australis	1	0	[03]	1	0	1	1	1
Carmichaelia compacta	1	0	3	1	0	1	1	1
Carmichaelia corrugata	2	1	3	1	0	1	1	1
Carmichaelia curta	1	0	3	1	0	1	1	1
Carmichaelia exsul	1	0	0	1	0	1	1	1
Carmichaelia hollowayi	2	1	3	1	0	1	1	1
Carmichaelia juncea	1	0	3	1	0	1	1	1
Carmichaelia kirkii	3	0	3	1	0	1	1	1
Carmichaelia monroi	2	0	0	1	0	2	1	1
Carmichaelia nana	2	0	0	1	0	2	1	1
Carmichaelia odorata	1	0	3	1	0	1	[01]	1
Carmichaelia petriei	1	0	1	0	1	1	1	1
Carmichaelia uniflora	2	1	3	1	0	1	1	1
Carmichaelia vexillata	2	0	?	1	0	2	1	1
Carmichaelia williamsii	1	0	0	1	0	1	1	1
Chordospartium muritai	1	0	1	1	1	2	1	1
Chordospartium stevensonii	1	0	1	1	1	2	1	1
Clianthus puniceus	1	0	0	1	0	1	0	1
Corallospartium crassicaule	1	0	1	1	1	1	1	1
Lessertia perennans	0	0	?	1	?	0	0	0
Notospartium carmichaeliae	1	0	2	1	1	2	1	1
Notospartium glabrescens	1	0	2	1	1	2	1	1
Notospartium torulosum	1	0	3	1	1	2	1	1
Sutherlandia frutescens	0	0	?	1	?	0	0	0
Swainsona cyclocarpa	0	0	?	0	?	1	0	0
Swainsona decurrens	0	0	?	0	?	0	0	0
Swainsona formosa	0	0	?	0	?	0	0	0
Swainsona galegifolia	0	0	0	0	0	0	0	0

	1	2	3	4	5	6	7	8
Swainsona kingii	0	0	?	0	?	1	0	0
Swainsona lessertiifolia	0	0	?	0	?	0	0	0
Swainsona microphylla	0	0	?	0	?	0	0	0
Swainsona novae-zelandiae	2	1	0	1	0	0	0	1
Swainsona oligophylla	0	0	?	0	?	1	0	0
Swainsona oroboides	0	0	?	0	?	1	0	0
Swainsona recta	0	0	?	0	?	0	0	0
Swainsona stipularis	0	0	?	0	?	1	0	0
Swainsona swainsonioides	0	0	?	0	?	0	0	0

	9	10	11	12	13	14	15	16
Astragalus bisulcatus	0	0	?	?	?	0	0	1
Biserrula pelecinus	0	0	?	?	?	0	0	1
Carmichaelia appressa	1	1	[34]	0	1	1	0	0
Carmichaelia arborea	1	1	[567]	0	1	1	1	0
Carmichaelia astonii	1	1	[012]	0	1	1	0	0
Carmichaelia australis	1	1	[456]	0	1	1	0	0
Carmichaelia compacta	1	1	[234]	0	1	1	0	0
Carmichaelia corrugata	1	1	[45678]	0	1	1	0	0
Carmichaelia curta	1	1	[234]	0	1	1	0	0
Carmichaelia exsul	1	1	[123]	0	1	1	0	0
Carmichaelia hollowayi	1	1	[123]	0	1	1	0	0
Carmichaelia juncea	1	1	[2345]	0	1	1	0	0
Carmichaelia kirkii	0	1	[3456]	0	1	1	0	0
Carmichaelia monroi	1	1	[123]	0	1	1	0	0
Carmichaelia nana	1	1	[23]	0	1	1	0	0
Carmichaelia odorata	1	1	[456]	0	1	1	1	0
Carmichaelia petriei	1	1	[23]	0	1	1	0	0
Carmichaelia uniflora	1	1	[34567]	0	1	1	0	0
Carmichaelia vexillata	1	1	[123]	0	1	1	0	0
Carmichaelia williamsii	1	1	[45]	0	1	1	0	0
Chordospartium muritai	1	1	[45]	1	1	1	2	0
Chordospartium stevensonii	1	1	[456]	1	1	1	2	0
Clianthus puniceus	0	[01]	?	0	1	1	0	0
Corallospartium crassicaule	1	1	[234]	0	1	1	1	0
Lessertia perennans	0	0	?	?	0	0	0	1
Notospartium carmichaeliae	1	1	[56]	1	1	1	2	0
Notospartium glabrescens	1	1	[345]	1	1	1	2	0
Notospartium torulosum	1	1	[234]	1	1	1	2	0
Sutherlandia frutescens	0	0	?	0	0	0	0	1
Swainsona cyclocarpa	0	0	?	?	0	0	0	1
Swainsona decurrens	0	0	?	0	0	0	0	1
Swainsona formosa	0	0	?	0	0	0	0	1
Swainsona galegifolia	0	0	?	?	0	0	0	1
Swainsona kingii	0	0	?	?	0	0	0	1

	9	10	11	12	13	14	15	16
Swainsona lessertiifolia	0	0	?	?	0	0	0	1
Swainsona microphylla	0	0	?	?	0	0	0	1
Swainsona novae-zelandiae	0	1	?	?	1	1	0	2
Swainsona oligophylla	0	0	?	?	0	0	0	1
Swainsona oroboides	0	0	?	?	0	0	0	2
Swainsona recta	0	0	?	?	0	0	0	1
Swainsona stipularis	0	0	?	?	0	0	0	1
Swainsona swainsonioides	0	0	?	?	0	0	0	1

	17	18	19	20	21	22	23	24
Astragalus bisulcatus	1	0	0	0	0	1	0	1
Biserrula pelecinus	1	1	0	0	0	1	0	1
Carmichaelia appressa	0	1	0	0	[01]	1	1	0
Carmichaelia arborea	0	2	0	0	0	1	0	1
Carmichaelia astonii	0	3	0	1	1	1	0	0
Carmichaelia australis	0	1	0	1	[01]	1	0	1
Carmichaelia compacta	0	3	0	0	0	1	0	1
Carmichaelia corrugata	0	3	0	0	1	1	0	0
Carmichaelia curta	0	2	0	1	0	1	0	1
Carmichaelia exsul	0	3	0	0	[01]	1	0	1
Carmichaelia hollowayi	0	2	0	1	1	1	0	1
Carmichaelia juncea	0	3	0	1	1	1	0	1
Carmichaelia kirkii	0	3	0	1	1	1	0	0
Carmichaelia monroi	0	3	0	1	1	1	0	0
Carmichaelia nana	0	3	0	1	1	1	0	1
Carmichaelia odorata	0	0	0	0	0	1	0	1
Carmichaelia petriei	0	2	0	1	[01]	1	0	1
Carmichaelia uniflora	0	3	0	0	1	1	0	0
Carmichaelia vexillata	0	3	0	1	1	1	0	0
Carmichaelia williamsii	0	3	0	1	0	1	0	0
Chordospartium muritai	0	0	1	1	0	2	0	1
Chordospartium stevensonii	0	0	1	1	1	2	0	0
Clianthus puniceus	0	1	0	0	2	1	0	0
Corallospartium crassicaule	0	0	1	1	1	2	0	0
Lessertia perennans	1	?	0	0	0	1	0	1
Notospartium carmichaeliae	0	0	0	0	[01]	1	0	0
Notospartium glabrescens	0	0	0	0	[01]	[01]	0	0
Notospartium torulosum	0	0	1	0	[01]	1	0	0
Sutherlandia frutescens	1	1	0	0	[01]	1	0	1
Swainsona cyclocarpa	1	2	0	0	1	[01]	1	0
Swainsona decurrens	2	3	0	0	1	1	1	0
Swainsona formosa	1	1	0	0	1	2	1	0
Swainsona galegifolia	2	0	0	0	1	0	1	0
Swainsona kingii	0	1	0	0	1	[01]	1	0

	17	18	19	20	21	22	23	24
Swainsona lessertiifolia	3	0	0	0	1	1	1	0
Swainsona microphylla	3	0	0	0	1	[01]	1	0
Swainsona novae-zelandiae	0	1	0	0	1	1	0	0
Swainsona oligophylla	1	0	0	0	1	1	1	0
Swainsona oroboides	1	2	0	0	1	2	1	0
Swainsona recta	3	0	0	0	1	1	1	1
Swainsona stipularis	2	0	0	0	1	1	1	1
Swainsona swainsonioides	3	2	0	0	1	1	1	1

	25	26	27	28	29	30	31	32
Astragalus bisulcatus	?	?	0	0	0	1	?	0
Biserrula pelecinus	?	?	0	0	0	[01]	?	0
Carmichaelia appressa	3	1	1	0	0	0	[23]	0
Carmichaelia arborea	6	2	1	0	0	0	[2345]	0
Carmichaelia astonii	2	[34]	1	1	0	0	[678]	0
Carmichaelia australis	3	1	1	0	0	0	[1234]	0
Carmichaelia compacta	1	1	1	0	0	0	[01]	0
Carmichaelia corrugata	2	[34]	1	0	0	0	[456]	0
Carmichaelia curta	1	1	1	0	0	0	[01]	0
Carmichaelia exsul	2	[34]	1	0	0	0	[1234]	0
Carmichaelia hollowayi	4	[23]	1	0	0	0	[01]	0
Carmichaelia juncea	1	1	1	0	0	0	0	0
Carmichaelia kirkii	2	3	1	1	0	0	[34]	0
Carmichaelia monroi	2	4	1	1	0	0	[6789]	0
Carmichaelia nana	0	[23]	1	0	0	0	[12]	0
Carmichaelia odorata	5	1	1	0	0	0	[01]	0
Carmichaelia petriei	4	1	1	0	0	0	[23]	0
Carmichaelia uniflora	2	[34]	1	0	0	0	[345]	0
Carmichaelia vexillata	2	?	1	1	0	0	[678]	0
Carmichaelia williamsii	7	5	1	0	0	0	[6789]	0
Chordospartium muritai	?	1	0	0	0	1	[01]	0
Chordospartium stevensonii	2	[23]	0	1	0	1	[12]	0
Clianthus puniceus	?	?	0	1	0	0	?	0
Corallospartium crassicaule	2	[23]	0	1	0	1	[12]	0
Lessertia perennans	?	?	0	1	0	0	?	0
Notospartium carmichaeliae	2	2	0	1	1	0	[234]	1
Notospartium glabrescens	2	[23]	0	1	1	0	[23]	0
Notospartium torulosum	2	3	0	1	1	0	[67]	1
Sutherlandia frutescens	?	?	0	1	0	0	?	0
Swainsona cyclocarpa	?	?	0	1	1	1	?	0
Swainsona decurrens	?	?	0	1	0	[01]	?	0
Swainsona formosa	?	?	0	1	0	1	?	0
Swainsona galegifolia	?	?	0	1	0	0	?	0
Swainsona kingii	?	?	0	1	0	[01]	?	0

	25	26	27	28	29	30	31	32
Swainsona lessertiifolia	?	?	0	1	0	1	?	0
Swainsona microphylla	?	?	0	1	0	0	?	0
Swainsona novae-zelandiae	?	?	0	1	0	1	?	0
Swainsona oligophylla	?	?	0	1	1	1	?	0
Swainsona oroboides	?	?	0	1	1	1	?	0
Swainsona recta	?	?	0	1	0	1	?	0
Swainsona stipularis	?	?	0	1	1	1	?	0
Swainsona swainsonioides	?	?	0	1	1	1	?	0

	33	34	35	36	37	38	39	40
Astragalus bisulcatus	?	1	0	1	0	2	0	0
Biserrula pelecinus	?	1	0	1	0	2	1	1
Carmichaelia appressa	1	0	1	1	1	[01]	0	0
Carmichaelia arborea	[12]	0	1	1	1	1	0	0
Carmichaelia astonii	[345]	0	1	1	1	0	0	1
Carmichaelia australis	[12]	0	1	1	1	[01]	0	0
Carmichaelia compacta	[01]	1	1	1	1	0	0	1
Carmichaelia corrugata	[23]	0	1	1	1	0	0	1
Carmichaelia curta	0	1	1	1	1	0	0	1
Carmichaelia exsul	[45]	0	1	1	1	[01]	0	0
Carmichaelia hollowayi	[12]	0	1	1	1	0	0	0
Carmichaelia juncea	0	1	1	1	1	0	0	1
Carmichaelia kirkii	[34]	0	1	1	1	0	0	0
Carmichaelia monroi	[23]	0	1	1	1	0	0	1
Carmichaelia nana	[01]	0	1	1	1	0	0	0
Carmichaelia odorata	1	0	1	1	1	1	0	0
Carmichaelia petriei	[12]	0	1	1	1	2	0	0
Carmichaelia uniflora	[23]	0	1	1	1	0	0	1
Carmichaelia vexillata	[34]	0	1	1	1	0	0	1
Carmichaelia williamsii	[678]	0	1	1	1	0	0	0
Chordospartium muritai	0	0	1	1	1	0	0	1
Chordospartium stevensonii	[01]	0	1	1	1	0	0	1
Clianthus puniceus	?	1	0	1	1	2	0	0
Corallospartium crassicaule	0	0	1	1	1	0	0	1
Lessertia perennans	?	0	0	0	0	2	0	0
Notospartium carmichaeliae	[567]	0	1	0	1	0	0	0
Notospartium glabrescens	[567]	0	1	1	1	0	0	0
Notospartium torulosum	[4567]	0	1	0	1	0	0	0
Sutherlandia frutescens	?	0	0	0	0	?	0	0
Swainsona cyclocarpa	?	1	0	1	?	1	1	?
Swainsona decurrens	?	1	0	0	0	0	?	1
Swainsona formosa	?	1	0	1	0	0	1	0
Swainsona galegifolia	?	1	0	0	0	0	0	0
Swainsona kingii	?	1	0	0	0	[01]	1	0

	33	34	35	36	37	38	39	40
Swainsona lessertiifolia	?	1	0	0	0	0	0	0
Swainsona microphylla	?	1	0	1	?	[01]	1	1
Swainsona novae-zelandiae	?	1	0	1	0	2	0	0
Swainsona oligophylla	?	1	0	0	?	0	1	?
Swainsona oroboides	?	1	0	0	0	[01]	1	0
Swainsona recta	?	1	0	1	?	2	0	?
Swainsona stipularis	?	1	0	1	0	1	1	0
Swainsona swainsonioides	?	1	0	1	?	1	1	?

	41	42	43	44	45	46	47
Astragalus bisulcatus	0	?	0	?	?	?	0
Biserrula pelecinus	1	?	0	?	?	0	0
Carmichaelia appressa	0	2	0	[12]	1	0	1
Carmichaelia arborea	0	1	1	[234]	0	0	1
Carmichaelia astonii	0	0	0	[2345]	0	0	1
Carmichaelia australis	0	2	0	[23]	1	[01]	1
Carmichaelia compacta	0	0	0	1	0	0	1
Carmichaelia corrugata	0	3	0	[12]	0	0	2
Carmichaelia curta	0	0	0	[012]	0	0	1
Carmichaelia exsul	0	2	0	[678]	1	1	1
Carmichaelia hollowayi	0	4	0	[34]	0	0	1
Carmichaelia juncea	0	0	0	[01]	0	0	1
Carmichaelia kirkii	0	4	0	[234]	0	1	1
Carmichaelia monroi	0	0	0	[23]	0	0	1
Carmichaelia nana	0	4	0	[23]	1	0	1
Carmichaelia odorata	0	1	1	[234]	0	0	1
Carmichaelia petriei	0	4	0	[123]	0	0	1
Carmichaelia uniflora	0	3	0	[12]	0	0	2
Carmichaelia vexillata	0	0	0	[23]	0	0	1
Carmichaelia williamsii	0	2	0	[5678]	1	1	1
Chordospartium muritai	0	0	0	1	0	1	1
Chordospartium stevensonii	0	0	0	[23]	0	1	1
Clianthus puniceus	0	?	0	?	0	0	1
Corallospartium crassicaule	0	0	0	[234]	0	1	1
Lessertia perennans	0	?	0	?	?	?	0
Notospartium carmichaeliae	1	0	0	[234]	0	1	1
Notospartium glabrescens	0	0	0	[234]	0	1	1
Notospartium torulosum	1	0	0	1	0	1	1
Sutherlandia frutescens	0	?	0	?	?	0	0
Swainsona cyclocarpa	0	?	0	?	?	?	1
Swainsona decurrens	0	?	0	?	?	?	?
Swainsona formosa	0	?	0	?	?	0	?
Swainsona galegifolia	0	?	0	?	?	0	1
Swainsona kingii	0	?	0	?	?	?	1

	41	42	43	44	45	46	47
Swainsona lessertiifolia	0	?	0	?	?	0	?
Swainsona microphylla	0	?	0	?	?	0	?
Swainsona novae-zelandiae	0	?	0	?	0	0	1
Swainsona oligophylla	0	?	0	?	?	?	?
Swainsona oroboides	0	?	0	?	?	0	?
Swainsona recta	0	?	0	?	?	?	?
Swainsona stipularis	0	?	0	?	?	?	1
Swainsona swainsonioides	0	?	0	?	?	?	?

Appendix 6. Vessel length and polymorphism overlap coding values for the phylogenetic analysis (n = 25).

Species	Vessel length (μm)																										Mean	Code
Ca. appressa	133	122	121	123	118	94	110	119	127	119	120	128	128	123	95	122	122	111	117	93	113	108	157	117	113		115.6±13.0	3,4
Ca. arborea	119	223	165	153	171	164	185	167	189	190	142	172	172	153	166	147	147	149	155	150	150	171	155	176	173		164.0±18.5	5-7
Ca. astonii	73	81	76	97	71	51	112	78	91	35	42	92	92	92	92	74	91	103	50	52	63	60	71	71	67		73.0±19.0	0-2
Ca. australis	159	153	147	153	147	96	170	163	148	141	150	150	145	113	136	150	121	152	148	166	83	171	164	142	136		143.0±21.0	4-6
Ca. compacta	134	161	136	127	113	86	73	67	112	131	115	88	104	94	134	83	104	142	96	103	83	126	135	131	139		110.5±24.5	2-4
Ca. corrugata	163	144	191	165	243	149	131	136	212	137	177	208	169	129	151	271	186	175	179	199	197	154	143	163	198		173.0±35.0	4-8
Ca. curta	84	140	140	140	119	104	132	105	117	117	117	117	73	91	99	83	137	83	114	82	75	114	152	115	79		107.0±23.0	2-4
Ca. exsul	96	83	113	89	100	109	64	89	93	115	70	85	82	86	80	96	90	77	72	90	77	99	81	94	106		88.5±13.5	1-3
Ca. hollowayi	153	68	89	89	55	116	65	78	104	101	96	81	81	80	89	71	85	62	106	104	130	125	73	124	114		92.0±24.5	1-3
Ca. juncea	173	173	116	145	136	122	119	100	106	93	115	115	120	103	73	128	107	123	161	161	161	84	159	88	90		121.0±29.0	2-5
Ca. kirkii	180	148	153	150	206	152	161	106	142	130	91	123	150	136	108	243	155	137	156	159	193	161	126	157	150		147.5±31.5	3-6
Ca. nana	82	87	79	93	93	101	82	74	100	95	120	104	97	89	108	96	84	84	73	80	90	117	105	103	82		90.5±12.0	2,3
Ca. monroi	60	60	93	98	92	102	86	73	124	118	67	74	72	49	85	76	106	130	117	117	102	102	89	114	93		90.0±21.5	1-3
Ca. odorata	129	132	159	150	139	132	166	118	201	157	166	152	136	161	152	129	169	169	148	150	164	181	151	137	216		153.0±23.0	4-6
Ca. petriei	92	88	103	96	87	81	97	97	116	79	92	102	114	108	92	122	98	122	83	84	90	101	78	78	139		96±15.5	2,3

Appendix 6 continued

Species	Vessel length (μm)																									Mean	Code
Ca. uniflora	178	141	167	130	109	228	167	170	174	146	214	210	194	208	146	146	185	172	99	130	152	123	128	89	127	154.5±36.5	3-7
Ca. vexillata	81	81	131	73	76	85	90	110	81	81	80	84	82	94	102	90	77	80	82	91	80	85	90	77	80	86.5±20.0	1-3
Ca. williamsii	115	139	156	166	149	134	165	128	151	145	142	145	179	118	137	142	139	139	139	120	179	128	144	149	104	142.0±18.0	4,5
Ch. muritai	147	143	134	126	152	167	181	130	123	121	165	148	132	164	137	126	128	118	162	132	128	130	116	137	112	136.0±17.5	2-4
Ch. stevensonii	136	109	128	162	167	150	151	109	162	160	163	161	148	106	161	151	166	152	177	155	151	116	109	100	120	143.5±22.5	4-6
Co. crassicaule	128	114	131	154	90	136	127	146	120	131	173	140	127	132	150	113	142	114	143	112	104	117	130	113	121	126.5±17.0	2-4
N. carmichaeliae	163	123	152	146	145	154	146	144	165	170	155	161	161	161	169	169	157	166	159	151	151	141	143	146	124	152.0±11.5	5,6
N. glabrescens	131	135	147	127	128	93	108	139	139	141	83	101	126	130	108	160	110	93	97	144	151	128	114	114	134	112.5±20.5	3-5
N. torulosum	114	107	99	124	131	103	127	100	89	121	124	111	133	87	94	86	100	99	70	100	89	132	100	102	100	103.5±17.5	2-4

Appendix 7. Keel length and polymorphism overlap coding values for the phylogenetic analysis (n = 10).

Species	Keel length (mm)										Mean	Code
Ca. appressa	3.5	3.5	3.7	3.7	3.8	3.9	3.6	3.8	3.6	3.7	3.68±0.13	1
Ca. arborea	5.4	5.8	5.5	5.5	5.3	5.6	5.8	5.3	5.7	5.4	5.53±0.18	2
Ca. astonii	10	10.8	10.1	11.4	11.6	11.7	10.3	10.4	10.5	10.2	10.7±0.64	3,4
Ca. australis	3.4	3.3	3.7	4.1	3.9	3.7	4.0	4.0	3.7	4.1	3.79±0.28	1
Ca. compacta	3.9	3.4	3.5	3.7	3.7	4.1	3.9	3.9	4.0	3.7	3.78±0.22	1
Ca. corrugata	7.8	8.3	9.6	8.8	8.5	8.0	8.0	8.5	8.2	8.1	8.38±0.52	3,4
Ca. curta	4.0	3.6	4.7	4.3	4.1	3.8	4.5	3.9	4.2	4.0	4.11±0.39	1
Ca. exsul	8.7	8.2	8.2	8.3	7.4	6.8	7.9	7.5	6.5	6.8	7.6±0.74	3,4
Ca. hollowayi	5.0	5.0	5.5	5.6	5.7	5.6	5.4	5.8	5.4	5.4	5.44±0.26	2,3
Ca. juncea	3.1	3.3	2.7	3.0	3.1	3.1	3.0	3.6	4.5	4.5	3.39±0.62	1
Ca. kirkii	9.0	8.9	8.2	9.0	8.9	8.8	9.3	8.8	8.8	9.0	8.87±0.27	3
Ca. nana	5.2	5.1	5.2	5.5	5.7	4.8	5.2	5.2	5.0	5.5	5.24±0.26	2,3
Ca. monroi	11.8	11.3	11.1	11.9	11.3	11.2	11.5	11.1	11.4	11.5	11.41±0.27	4
Ca. odorata	3.9	4.0	3.8	3.9	4.2	3.9	4.0	3.9	4.0	4.1	3.97±0.11	1
Ca. petriei	4.1	4.2	4.5	4.3	4.3	3.9	4.3	4.3	3.6	4.3	4.18±0.25	1
Ca. uniflora	7.8	8.4	8.1	8.1	7.8	7.8	7.8	7.4	8.4	8.0	7.96±0.30	3,4
Ca. vexillata	-	-	-	-	-	-	-	-	-	-	-	-
Ca. williamsii	28.0	29.0	29.0	27.0	29.0	29.0	25.0	27.0	26.0	28.0	27.7±1.41	9
Ch. muritai	3.5	3.2	3.0	3.5	3.5	3.5	3.4	3.3	3.5	3.6	3.4±0.20	1
Ch. stevensonii	7.8	7.8	7.6	8.5	8.0	7.0	7.1	7.0	7.0	7.2	7.5±0.50	2,3
Co. crassicaule	8.0	7.5	8.5	8.0	8.2	8.6	8.0	8.8	8.3	8.2	8.21±0.36	2,3
N. carmichaeliae	7.7	7.0	6.5	6.5	7.0	7.7	7.8	6.9	6.8	6.0	7.0±0.06	2
N. glabrescens	7.8	8.5	5.5	6.0	5.8	8.2	7.9	8.7	8.4	9.0	7.6±1.30	2,3
N. torulosum	7.8	8.2	8.1	8.4	8.3	8.1	8.5	8.4	8.6	8.2	8.26±0.20	3

Appendix 8. Ovule numbers and polymorphism overlap coding values for the phylogenetic analysis (n = 10).

Species	Ovule numbers										Mean	Code
Ca. appressa	8	8	9	6	8	8	7	8	8	8	7.77±0.83	2, 3
Ca. arborea	8	9	8	8	6	10	10	11	12	10	9.2±1.75	2-5
Ca. astonii	16	13	14	14	11	13	13	13	14	14	13.4±1.33	6-8
Ca. australis	12	9	6	8	6	6	6	6	7	7	7.3±1.94	1-4
Ca. compacta	5	6	6	4	5	5	6	5	6	4	5.2±0.78	0,1
Ca. corrugata	11	11	10	13	11	12	12	10	12	12	11.4±0.96	4-6
Ca. curta	5	5	6	6	7	6	6	5	5	6	5.7±0.67	0,1
Ca. exsul	6	6	6	7	7	10	11	8	7	-	7.5±1.80	1-4
Ca. hollowayi	8	3	6	6	8	7	7	7	6	5	6.3±1.49	0-2
Ca. juncea	6	6	3	4	5	4	3	3	4	3	4.1±1.19	0
Ca. kirkii	9	10	8	9	8	9	9	10	9	8	8.9±0.73	3,4
Ca. nana	6	6	8	6	6	8	7	8	8	4	6.7±1.09	1,2
Ca. monroi	15	12	14	18	14	13	15	14	15	15	14.5±1.58	6-9
Ca. odorata	4	5	4	5	4	8	9	10	7	11	6.7±1.47	0-3
Ca. petriei	8	7	6	8	8	8	7	7	7	9	7.5±0.85	2,3
Ca. uniflora	9	10	12	9	10	9	11	8	10	10	9.8±1.13	3-5
Ca. vexillata	16	14	12	15	14	14	14	11	14	15	13.9±1.45	6-8
Ca. williamsii	17	16	16	15	15	12	12	13	14	15	14.5±1.71	6-9
Ch. muritai	6	5	5	5	5	4	5	5	5	5	5.0±0.5	0,1
Ch. stevensonii	6	7	7	7	6	7	6	8	5	8	6.7±1.2	1,2
Co. crassicaule	6	6	7	6	7	5	5	6	6	6	6.0±0.16	1,2
N. carmichaeliae	10	10	11	10	9	8	10	7	8	8	9.1±1.2	2-4
N. glabrescens	9	9	9	8	8	8	7	9	9	8	8.4±0.7	2,3
N. torulosum	13	13	13	13	11	13	12	14	14	13	12.9±0.9	6,7

Appendix 9. Fruit length and polymorphism overlap coding values for the phylogenetic analysis (n = 20).

Species	Fruit length (mm)																				Mean	Code
Ca. appressa	8.0	8.5	7.5	7.5	8.0	7.5	8.5	6.5	7.5	8.0	-	-	-	-	-	-	-	-	-	-	7.70±0.65	1
Ca. arborea	10.0	10.0	9.0	10.0	9.0	11.0	9.0	9.5	9.0	9.0	9.5	9.0	8.5	10.0	9.0	12.0	8.0	9.0	13.5	10.0	9.50±1.21	1,2
Ca. astonii	8.5	19.0	19.5	20.5	21.5	20.0	17.0	19.0	19.5	16.0	18.0	17.5	15.0	17.0	14.0	15.0	15.0	15.0	13.5	14.0	17.20±2.42	3-5
Ca. australis	10.0	10.0	12.0	11.5	9.0	8.0	9.5	5.0	6.5	6.5	8.0	10.5	8.5	8.0	8.0	7.0	7.5	8.0	9.5	10.0	8.70±1.70	1,2
Ca. compacta	5.5	6.0	5.0	5.0	6.0	6.0	6.0	5.0	5.0	5.5	6.0	5.5	5.0	6.0	4.5	5.0	4.5	4.5	5.0	5.5	5.30±0.55	0,1
Ca. corrugata	11.0	9.0	10.0	11.0	11.0	11.0	10.0	11.0	11.0	9.0	12.5	13.0	11.0	13.5	12.0	11.5	11.5	12.5	11.0	12.0	11.60±1.48	2,3
Ca. curta	3.5	3.5	3.0	4.0	4.0	3.0	5.0	4.5	3.0	3.5	4.5	4.0	4.0	3.5	4.5	4.0	4.0	3.5	4.0	3.5	3.80±0.60	0
Ca. exsul	16.0	17.0	16.5	18.0	18.5	18.5	15.5	19.0	15.5	18.5	-	-	-	-	-	-	-	-	-	-	17.3±1.35	4,5
Ca. hollowayi	10.0	10.0	9.0	8.5	9.0	10.0	9.5	9.5	9.5	8.5	8.5	8.5	9.0	9.5	10.0	10.0	8.5	10.0	10.0	9.0	9.34±0.62	1,2
Ca. juncea	3.0	4.0	4.5	5.0	3.5	4.0	4.0	3.0	3.0	2.5	4.0	4.5	4.0	4.0	4.0	5.0	5.0	5.0	5.0	3.5	4.09±0.76	0
Ca. kirkii	17.0	15.0	16.0	13.0	15.0	13.0	17.0	12.5	14.0	10.0	10.0	17.5	16.5	14.0	14.0	12.0	14.0	15.0	12.5	16.0	14.17±2.10	3,4
Ca. nana	8.5	5.0	7.0	7.0	6.5	6.5	6.0	6.5	7.0	5.5	4.5	5.2	5.0	7.0	5.0	6.0	6.5	5.5	6.0	6.0	6.14±1.09	0,1
Ca. monroi	13.0	14.0	12.0	12.5	13.5	12.0	12.5	12.0	11.5	11.5	14.5	17.0	15.0	12.5	14.0	13.5	10.5	14.5	13.5	10.5	13.12±1.52	2,3
Ca. odorata	6.0	7.0	8.0	7.5	8.0	6.0	6.0	7.0	7.0	8.5	8.0	6.0	8.0	6.0	8.0	7.0	6.5	6.0	6.0	5.0	6.72±1.05	1
Ca. petriei	7.5	7.0	8.5	8.0	7.0	7.5	6.5	7.5	6.5	9.5	7.0	8.0	7.0	8.0	6.5	8.0	9.0	6.5	7.5	9.5	7.79±1.10	1,2

Appendix 9 continued

Species	Fruit length (mm)																				Mean	Code
Ca. uniflora	12.0	13.0	12.0	12.5	12.0	13.0	17.0	15.0	16.5	14.5	12.0	12.5	11.0	12.0	12.5	11.0	12.0	11.0	12.0	12.0	12.90±1.63	2,3
Ca. vexillata	15.5	15.5	17.5	16.0	17.0	17.0	13.0	10.5	12.5	14.0	14.0	12.0	10.0	15.0	17.0	17.0	12.0	19.0	14.0	12.0	14.45±2.50	3,4
Ca. williamsii	28.0	31.0	24.0	23.0	23.0	23.0	25.0	25.0	22.0	27.0	21.0	27.0	25.0	27.0	27.0	24.0	28.0	34.0	26.0	28.0	26.8±3.46	6-8
Ch. muritai	4.0	4.1	4.5	4.0	4.5	3.5	4.0	4.0	4.0	3.5	4.5	4.0	4.0	4.0	4.0	3.5	4.0	4.0	4.0	3.5	3.99±0.20	0
Ch. stevensonii	5.5	5.5	6.0	5.0	4.5	5.0	6.0	5.0	5.5	5.0	5.0	5.0	5.0	5.5	5.5	6.0	5.5	5.0	5.5	6.0	5.36±0.43	0,1
Co. crassicaule	5.0	5.0	5.0	5.0	5.0	6.0	5.0	4.5	5.0	5.0	5.0	-	-	-	-	-	-	-	-	-	5.04±0.35	0
N. carmichaeliae	18.0	25.0	21.0	19.0	20.0	20.0	24.0	20.0	22.0	27.0	21.0	20.0	19.0	22.0	27.0	24.0	28.0	31.0	27.0	25.0	23.0±3.62	5-7
N. glabrescens	20.0	23.0	25.0	22.0	15.0	16.0	17.0	30.0	24.0	21.0	20.0	27.0	24.0	26.0	20.0	25.0	21.0	20.0	19.0	31.0	23.44±4.5	5-7
N. torulosum	20.0	21.0	22.0	24.0	26.0	24.0	22.0	18.0	16.0	19.0	18.0	17.0	18.0	23.0	30.0	29.0	23.0	22.0	23.0	21.0	21.75±3.74	4-7

Appendix 10. Seed length and polymorphism overlap coding values for the phylogenetic analysis (n = 20).

Species	Seed length (mm)																				Mean	Code
Ca. appressa	2.0	1.8	2.1	2.1	1.8	1.9	2.0	2.2	1.9	2.0	1.7	1.8	1.9	1.7	1.9	1.9	2.0	2.0	2.1	1.5	1.91±0.16	1,2
Ca. arborea	3.2	2.9	2.7	2.0	2.5	2.5	2.3	2.8	2.7	2.2	2.5	2.4	2.5	2.5	2.5	2.6	3.2	2.8	2.6	2.7	2.60±0.29	2-4
Ca. astonii	3.0	3.5	3.0	3.0	3.0	4.2	3.0	3.0	3.0	3.1	2.7	2.1	3.1	2.4	2.5	2.6	2.8	2.3	2.1	2.9	2.86±0.0.50	2-5
Ca. australis	2.5	2.8	2.3	2.0	2.2	2.2	2.1	2.1	2.5	2.6	2.6	2.4	2.7	3.1	2.8	2.6	2.3	2.3	1.5	1.3	2.29±0.34	2,3
Ca. compacta	1.7	1.7	2.0	1.8	1.9	1.8	1.8	1.8	1.8	1.9	2.0	2.1	1.9	1.7	1.8	1.9	1.9	1.8	1.8	1.8	1.84±0.10	1
Ca. corrugata	1.9	2.3	1.8	2.3	2.3	2.1	2.3	2.1	2.2	2.0	1.9	2.2	2.1	2.2	1.9	2.2	2.3	2.2	2.0	2.1	2.11±0.15	1,2
Ca. curta	1.6	2.0	1.4	1.7	1.9	2.0	1.7	2.1	2.2	2.2	1.6	1.4	1.6	2.2	1.9	1.6	1.2	2.2	1.7	2.0	1.81±0.30	0-2
Ca. exsul	4.6	3.5	3.9	3.9	4.5	4.4	4.5	4.2	4.3	4.1	4.1	-	-	-	-	-	-	-	-	-	4.18±0.32	6-8
Ca. hollowayi	3.0	2.4	2.6	2.9	3.0	3.1	2.2	2.7	2.8	2.5	2.6	3.0	2.7	2.7	3.0	2.9	2.5	2.6	2.7	2.3	2.71±0.25	3,4
Ca. juncea	1.4	1.5	1.5	1.6	1.5	1.5	1.6	1.4	1.2	1.6	1.9	1.5	1.4	1.4	1.4	1.5	1.5	1.3	1.5	1.4	1.48±0.14	0,1
Ca. kirkii	2.5	2.6	2.7	2.7	2.1	2.4	2.5	2.7	2.7	3.3	2.3	2.6	2.4	2.4	2.5	2.5	2.5	2.3	2.0	2.5	2.51±0.27	2-4
Ca. nana	2.2	2.1	1.8	2.0	2.0	2.5	2.1	2.4	2.4	2.2	2.0	2.1	2.5	2.1	2.2	2.4	2.5	2.0	2.3	.2.2	2.2±0.20	2,3
Ca. monroi	2.3	1.9	2.3	2.5	2.3	2.3	2.5	2.5	2.7	2.3	2.3	2.5	2.3	2.3	2.2	1.9	2.2	2.3	2.4	1.9	2.29±0.21	2,3
Ca. odorata	2.6	2.9	2.2	2.4	2.2	2.9	2.4	2.6	2.2	2.5	2.2	2.6	2.2	2.5	2.7	2.3	2.7	2.6	2.9	2.3	2.53±0.26	2-4
Ca. petriei	2.6	2.5	1.9	2.0	2.5	2.6	2.0	2.2	2.3	2.0	1.8	2.3	2.2	1.9	1.8	1.6	2.0	2.1	1.5	1.8	2.08±0.31	1-3

Appendix 10 continued

Species	Seed length (mm)																				Mean	Code
Ca. uniflora	2.3	2.4	2.0	2.2	2.2	2.0	2.0	2.4	1.9	2.2	2.2	1.9	2.3	1.8	2.2	2.1	2.2	2.0	2.2	2.0	2.12±0.16	1,2
Ca. vexillata	2.1	2.6	2.2	2.1	2.0	2.1	2.2	2.3	2.1	2.1	2.4	2.6	2.3	2.1	2.3	2.4	2.2	2.3	2.2.	2.3	2.24±0.16	2,3
Ca. williamsii	5.1	5.0	4.7	3.7	3.3	3.2	5.0	3.6	4.0	4.3	3.4	4.1	3.6	3.6	3.5	4.9	4.3	4.3	4.2	3.8	4.07±0.58	5-8
Ch. muritai	1.7	1.8	1.8	1.8	1.7	1.8	1.8	1.7	1.4	1.8	1.9	1.4	1.7	1.6	1.7	1.8	1.7	1.7	1.7	1.8	1.73±0.10	1
Ch. stevensonii	2.3	2.3	2.0	2.5	2.1	2.3	2.4	2.9	3.0	2.4	2.2	2.3	2.3	2.1	2.5	2.2	2.3	2.1	2.7	2.4	2.36±0.25	2,3
Co. crassicaule	2.3	2.1	2.5	3.0	2.6	2.8	2.9	2.5	2.7	2.7	2.3	2.6	2.4	2.8	2.3	2.8	2.6	2.5	3.0	3.1	2.62±0.26	2-4
N. carmichaeliae	2.0	1.7	1.7	1.7	1.6	1.7	1.6	1.7	1.5	1.6	1.7	1.7	2.0	1.6	1.7	1.7	1.6	1.6	1.5	1.7	1.68±0.13	0,1
N. glabrescens	3.1	2.4	2.4	2.5	2.7	2.7	2.5	2.8	2.0	2.4	2.4	2.9	2.4	1.8	2.8	2.5	2.8	2.9	2.4	1.8	2.51±0.34	2-4
N. torulosum	1.8	1.5	1.7	1.8	1.8	1.8	1.7	1.6	1.9	1.7	1.8	1.5	1.6	1.6	1.8	1.6	1.8	1.9	1.6	2.0	1.73±0.14	1

Appendix 11 Character attributes for reweighted analyses of 47 and 42 character data matrices. The number of character states, actual number of steps per character, rescaled consistency index, and the final weight.

Character		Complete character set, 47 characters, Fig. 6.2.			Reduced character set, 42 characters, Fig. 6.3D.		
Number	States	Steps	RCI	Weight (×1000)	Steps	RCI	Weight (×1000)
1	4	5	0.533	533	6	0.417	417
2	2	3	0.0	0	3	0.000	0
3	4	6	0.333	333	7	0.238	238
4	2	2	0.462	462	2	0.462	462
5	2	1	1.0	1000	1	1.0	1000
6	3	7	0.202	202	6	0.255	255
7	2	1	1.0	1000	1	1.0	1000
8	2	1	1.0	1000	1	1.0	1000
9	2	1	1.0	1000	1	1.0	1000
10	2	1	1.0	1000	1	1.0	1000
11	7	6	0.067	67	-	-	-
12	2	2	0.375	375	2	0.375	375
13	2	1	1.0	1000	1	1.0	1000
14	2	1	1.0	1000	1	1.0	1000
15	3	3	0.556	556	3	0.566	566
16	3	3	0.619	619	3	0.619	619
17	4	7	0.273	273	7	0.273	273
18	4	13	0.121	121	13	0.121	121
19	1	2	0.333	333	2	0.333	333
20	1	7	0.065	65	7	0.065	65
21	2	6	0.167	167	6	0.167	167
22	2	4	0.250	250	4	0.256	256
23	1	1	1.0	1000	1	1.0	1000
24	1	6	0.118	118	7	0.092	92

Appendix 11 continued

Number	States	Steps	RCI	Weight	Steps	RCI	Weight
25	8	7	1.0	1000	7	1.0	1000
26	5	6	0.500	500	-	-	-
27	2	2	0.464	464	2	0.464	464
28	2	4	0.200	200	5	0.147	147
29	2	2	0.429	429	2	0.429	429
30	2	5	0.133	133	5	0.133	133
31	10	9	0.083	83	-	-	-
32	2	1	1.0	1000	1	1.0	1000
33	9	5	0.700	700	-	-	-
34	2	3	0.296	296	3	0.296	296
35	2	1	1.0	1000	1	1.0	1000
36	2	5	0.100	100	5	0.100	100
37	2	1	1.0	1000	1	1.0	1000
38	3	5	0.280	280	5	0.280	280
39	2	2	0.438	438	2	0.438	438
40	2	7	0.057	57	5	0.120	120
41	2	2	0.250	250	2	0.250	250
42	5	6	0.476	476	4	1.0	1000
43	2	1	1.0	1000	1	1.0	1000
44	9	5	0.160	160	-	-	-
45	2	3	0.167	167	1	1.0	1000
46	2	2	0.438	438	3	0.250	250
47	3	2	1.0	1000	2	1.0	1000